



Variation in late holocene marine environments in the Canadian Arctic Archipelago: Evidence from ringed seal bone collagen stable isotope compositions

Paul Szpak ^{a,*}, James M. Savelle ^b, James Conolly ^a, Michael P. Richards ^c

^a Department of Anthropology, Trent University, Peterborough, ON, K9L 0G2, Canada

^b Department of Anthropology, McGill University, Montreal, QC, H3A 2T7, Canada

^c Department of Archaeology, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada

ARTICLE INFO

Article history:

Received 28 May 2018

Received in revised form

7 March 2019

Accepted 11 March 2019

Available online 27 March 2019

Keywords:

Stable isotopes

Arctic

Seals

Climate change

Sea ice

Archaeology

Paleoeskimo

Dorset

Thule

ABSTRACT

Environmental change in the Arctic has been a primary topic of interest in recent years, particularly as it relates to the consequences of anthropogenic climate change. Sea ice is of particular importance in this context, both in terms of the effects of climate change in the Arctic, but also globally. Most studies examining the responses of various components of the biosphere to warming temperatures necessarily have a short temporal perspective. The purpose of this study was to use stable isotopes to examine long-term variation (c. 4000–500 yr BP) in the ecology of a ubiquitous Arctic marine mammal (the ringed seal, *Pusa hispida*) that is intimately linked to sea ice. We present $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for ringed seal bone collagen from archaeological sites in the central Canadian Arctic Archipelago as well as 61 new AMS ^{14}C dates from these sites. Ringed seal $\delta^{13}\text{C}$ values increased between the earliest sites in our study, Early Pre-Dorset (c. 4000 cal yr BP), through to the Late Dorset period (c. 800 cal yr BP) suggesting increasing primary productivity derived from sea ice relative to phytoplankton over this period and an overall cooling trend. Between the Late Dorset (1500–700 yr BP) and Thule (c. 700–500 yr BP) periods there was an abrupt decline in the contribution of sea ice algae to higher trophic levels, consistent with reduced sea ice extent and increased open water conditions. These data demonstrate the potential of using marine mammals from archaeological sites to reconstruct the changing importance of sea ice to food webs over time and offer insight into the consequences of climatic variation at higher trophic levels, which is difficult if not impossible to obtain with other proxy records.

© 2019 Elsevier Ltd. All rights reserved.

1. Introduction

A great deal of recent research has focused on the dynamics of sea ice-associated ecosystems, driven in large part by the widespread observations of decreasing sea ice extent in the Arctic linked to recent anthropogenic climate change (Kirchmeier-Young et al., 2016; Mueller et al., 2018; Najafi et al., 2015; Stroeve et al., 2007, 2012). Sea ice dynamics are critical to polar environments because sea ice is extremely important from both a physical and biogeochemical perspective (Dieckmann and Hellmer, 2010; Moore and Huntington, 2008; Tynan et al., 2010). Sea ice can cover up to 7% of the surface area of the Earth (Comiso, 2010), making it a spatially

extensive and very important biome (Dieckmann and Hellmer, 2010). Globally, it exerts a tremendous influence on the state of the atmosphere and the ocean. Salinity and the vertical stratification of ocean water are strongly influenced by sea ice during formation and melting (Aagaard and Carmack, 1989; Aagaard et al., 1981). Many of the strongest impacts of recent warming on the marine biosphere have been observed to be or are expected to be driven by the decreased extent of sea ice and associated biological productivity (Grebmeier et al., 2006; Harada, 2016; Kędra et al., 2015; Moore and Reeves, 2018).

Atmospheric conditions are impacted by sea ice by virtue of its surface albedo. As light snow and ice surfaces are lost due to melting, less solar radiation is reflected back into the atmosphere and is instead absorbed by the darker ocean surface (Curry et al., 1995; Maykut and Untersteiner, 1971; Screen et al., 2018). As conditions warm, the ice-free summer season is longer and ice forms

* Corresponding author.

E-mail address: paul.szpak@gmail.com (P. Szpak).

2. Environmental context

[illegible]

Sea ice algae enters the food web primarily through the consumption of suspended particulate organic matter by pelagic grazers (Michel et al., 1996; Søreide et al., 2006, 2008), as well as through feeding by benthic (bottom-associated) organisms following sedimentation (Boetius et al., 2013; McMahon et al., 2006; Renaud et al., 2007; Werner, 1997). Direct grazing on attached ice algae by sea ice meiofauna appears to be relatively insignificant with respect to the transfer of nutrients to higher trophic levels (Nozais et al., 2001; Werner, 1997). Copepods

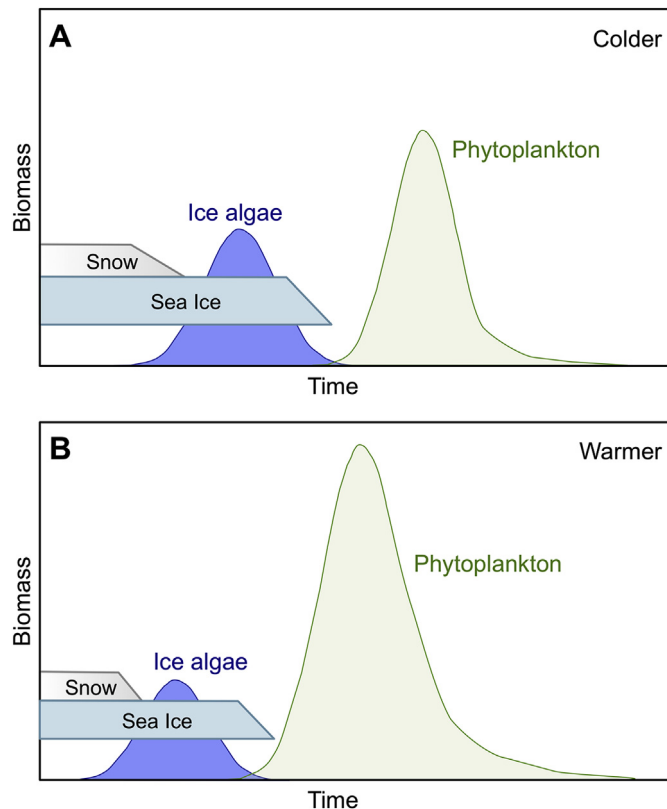


Fig. 2. Generalized schematic showing the relative importance of primary production derived from sea ice algae and pelagic phytoplankton under relatively cold (A) and relatively warm (B) conditions (adapted from Ji et al., 2013; Leu et al., 2011). Note that the relative sizes of the peaks have been exaggerated to more clearly illustrate the differences between the two, which are likely to be subtler.

(zooplankton) of the genus *Calanus* (calanoid copepods) are quantitatively the most important consumers that transfer primary production to higher trophic levels throughout the Arctic (Darnis et al., 2012). Calanoid copepods are herbivorous and they consume both phytoplankton and sea ice algae (Durbin and Casas, 2014; Forest et al., 2011a; Kohlbach et al., 2016). They are especially lipid rich (>70% by dry weight) and provide extremely energy-rich packages to higher trophic levels (Falk-Petersen et al., 2007, 2009). These copepods are the primary prey of Arctic cod (*Boreogadus saida*) (Benoit et al., 2010; Bradstreet et al., 1986; Hobson and Welch, 1992), little auks (*Alle alle*) (Bradstreet, 1982; Hobson, 1993; Karnovsky et al., 2008), and bowhead whales (*Balaena mysticetus*) (Laidre et al., 2007; Pomerleau et al., 2011, 2012). Arctic cod are very important prey items for marine mammals and birds, particularly ringed seals, serving as the most important link between primary and tertiary consumers (Bradstreet and Cross, 1982; Hop and Gjosæter, 2013; Welch et al., 1992, 1993). Arctic cod biomass has been observed to be high in the CAA (Bradstreet et al., 1986; Crawford and Jorgenson, 1996; Hop et al., 1997), with dense schools occurring near shore in the summer months (Welch et al., 1992).

The ringed seal is a small (50–70 kg for adults) pinniped with a Holarctic distribution and is the most abundant marine mammal in the Arctic (McLaren, 1958; Reeves, 1998; Smith et al., 1991). Its life history is strongly tied to sea ice and even during the fall and winter it remains under the landfast ice by maintaining a series of breathing holes. Females give birth in March through April in dens of excavated snow above these breathing holes (Smith and Stirling, 1975). During the open water season ringed seals forage to a greater

extent in pelagic environments relative to the period of extensive ice cover when they rely to a greater extent on sympagic and benthic prey (Young and Ferguson, 2013). Ringed seals are not highly specialized feeders and there is variation in their diet across their geographic range, but Arctic cod tends to be the most abundant prey item (Born et al., 2004; McLaren, 1958; Siegstad et al., 1998), particularly in the CAA (Bradstreet and Cross, 1982). Other ringed seal prey items include amphipods (especially *Themisto libellula* but also *Gammarus* sp.), mysids (*Mysis* sp.), sculpins (Cottidae), bivalves, cephalopods, and shrimp (Holst et al., 2001; Matley et al., 2015).

The ringed seal was the focus of this study for two reasons. First, it is by far the most abundant marine taxon across a large temporal and spatial scale in archaeological assemblages from across the Canadian Arctic (Darwent, 2001; Moody and Hodgetts, 2013; Murray, 1999). It is therefore relatively easy to generate a robust sample size for the majority of sites with reasonably large faunal assemblages. Second, because of its strong association with sea ice, this species should be sensitive to changing environmental conditions and particularly changes related to its sea ice habitat (Ferguson et al., 2005; Hamilton et al., 2015, 2017; Laidre et al., 2008). Because of its widespread distribution, abundance, and importance as both a predator (of Arctic cod) and prey (of polar bears), the ringed seal has been characterized as a keystone species in the Arctic (Hamilton et al., 2015; Luque et al., 2014).

3. Archaeological context

The faunal material analyzed in this study can be divided into four temporal phases: pre-Dorset (c. 4000–2800 cal yrs BP), Early/Middle Dorset (2800–1500 cal yrs BP), Late Dorset (1500–700 cal yrs BP), and Thule (700–500 cal yrs BP). There were two major human migrations into the Canadian Arctic, the first beginning around 5200 cal yrs BP by a group of highly mobile hunter-gatherers that originated in the Bering Strait region (Milne and Park, 2016). Traditionally, this group of people has been referred to as Paleoeskimo in the archaeological literature, but this term is now seen as pejorative and in this paper we avoid its use (see Hodgetts and Wells, 2016). The earliest expansion into the Canadian Arctic is generally believed to have coincided with a warm period (Barry et al., 1977; Darwent, 2001; Dekin, 1972). The sites associated with these early groups are typically small and ephemeral; substantial middens are therefore usually lacking, but there are some exceptions (e.g., Darwent, 2001; McGhee, 1979; Murray, 2005). While there was variability in the types of faunal resources exploited through time (e.g., walrus is nearly absent in the earliest periods, but reasonably abundant in late periods; Dyke et al., 1999), ringed seal is consistently among the most important taxa, or the most important taxon, at coastal sites (Darwent, 2001; Murray, 1999). Between the earliest settlement of the Canadian Arctic and A.D. 1000, there were significant human demographic oscillations with entire regions being abandoned for several centuries at a time (Dyke and Saville, 2009; Dyke et al., 2011; Saville and Dyke, 2002, 2009, 2014). Notably, these oscillations serve to limit the temporal coverage of paleoenvironmental studies such as this one as there are no archaeofaunal materials to sample from these intervals.

Between approximately A.D. 1000 and 1300 the Late Dorset occupants of the Canadian Arctic disappeared. There is no evidence supporting their integration, at least on a biological level, into the incoming Thule groups (Raghavan et al., 2014), who arrived in the Canadian Arctic from Alaska around A.D. 1200 (Friesen and Arnold, 2008). The CAA was then populated by Thule groups between A.D. 1300 and 1450. This period is often described as 'Classic Thule' and is characterized by substantial dwelling features and middens, and abundant bowhead whale remains in some regions, often

incorporated as architectural elements (Savelle, 1997, 2002, 2010). A greater extent of open water in the central Canadian Arctic coincident with the 'Medieval Warm Period' (c. A.D. 950–1250) and the abundance of bowhead whales have been cited as motivating factors for the migration of the Thule from west to east (Barry et al., 1977; Dekin, 1972; McCartney, 1977; McGhee, 1969/1970). Nonetheless, even Thule sites in the core of the bowhead hunting area tend to have faunal assemblages that are dominated by ringed seal (Iorio, 2005; Rick, 1980; Savelle and McCartney, 1988). The period after A.D. 1450 is frequently denoted 'Modified Thule' and is associated with a cessation of bowhead hunting, possibly caused by the initiation of the much colder conditions and increased sea ice extent of the 'Little Ice Age' (McCartney, 1977; McGhee, 1969/1970; Schledermann, 1979). None of the materials sampled as part of this study, however, are associated with this later phase and instead the Thule samples can all be placed within the Classic Thule phase predating A.D. 1450.

4. Isotopic context

Stable isotope studies of archaeological and paleontological vertebrate fauna have become increasingly common and are recognized as an important source of paleoenvironmental data. Generally, such paleoenvironmental studies have focused almost exclusively on terrestrial environments and a vast literature on this topic exists (Koch et al., 2009). Far fewer studies have used isotopic measurements of vertebrate remains to reconstruct aspects of past marine environments. These studies have focused on the foraging ecology, and changes therein, of particular species in the late Holocene and historic periods (Burton et al., 2001; Gorlova et al., 2012; Krylovich, 2011; Moss et al., 2006; Ostrom et al., 2017; Szpak et al., 2012; Vales et al., 2017; Wiley et al., 2013). Relatively little attention has been paid to the potential for isotopic measurements of marine vertebrate archaeofaunal remains to record environmental changes from a bottom-up perspective in marine environments – i.e., changes in the relative importance of different producers, nutrient regime shifts, rates of primary productivity, and other oceanographic factors (but see Braje et al., 2017; Misarti et al., 2009; Szpak et al., 2018; Szpak et al., 2013; Ukkonen et al., 2014). Nonetheless, it is well established that large-scale carbon and nitrogen isotopic variations exist in marine producers and the nutrients that they utilize (Altabet, 2006; France, 1995; Montoya, 2008; Rau et al., 1982; Sigman et al., 2009) and these variations are reflected in the tissues of higher trophic level consumers (Duggins et al., 1989; Hamilton et al., 2011; Ruiz-Cooley and Gerrodette, 2012; Takai et al., 2000; Wallace et al., 2006). The remainder of this section provides an overview of this isotopic variation in the marine environment, with an emphasis on the Arctic.

Carbon isotopic compositions are largely conserved across trophic levels (McConnaughey and McRoy, 1979), but there is significant variation within and among classes of producers (Raven et al., 2002). Offshore and open water marine environments are dominated by pelagic phytoplankton and in some cases N_2 -fixing bacteria (Capone et al., 1997), but in the inshore or nearshore environments exploited by ancient human populations, benthic and macrophyte algae are quantitatively important contributors to food webs (Duggins et al., 2016). These different sources of production tend to be isotopically distinct and this distinction is usually ascribed to either differences in the discrimination against ^{13}C during CO_2 uptake influenced by variable thickness of the algal boundary layer driven by differing levels of water turbidity (France, 1995; Osmond et al., 1981) or variable utilization of dissolved bicarbonate relative to CO_2 , the former of which is enriched in ^{13}C by ~9‰ compared to the latter (Kroopnick, 1985; Maberly et al., 1992; Mook et al., 1974).

As discussed above, in the Arctic and Antarctic, the two important sources of production are pelagic phytoplankton and ice-associated algae (commonly called sea ice algae) (Gradinger, 2009). Sea ice algae have $\delta^{13}C$ values that are 5–12‰ higher than pelagic phytoplankton (France et al., 1998; Hobson et al., 1995; Søreide et al., 2006) a distinction that is similar to or slightly larger than that between kelp and phytoplankton (Duggins et al., 1989). As with kelp, the relative importance of pelagic and sympagic production can be approximated on the basis of consumer $\delta^{13}C$ values (Kohlbach et al., 2016; Søreide et al., 2006, 2013; Tamelander et al., 2006), including taxa that feed at high trophic levels (McMullin et al., 2017; Wang et al., 2016). As discussed above, ice algae bloom prior to phytoplankton in the Arctic. This is significant because bone collagen isotopic compositions should capture equally the contribution of production derived from sea ice algae and from phytoplankton because of the slow rate of turnover (Hedges et al., 2007; Riofrío-Lazo and Aurióles-Gamboa, 2013). This is not true of many of the metabolically active tissues that are frequently sampled in ecological studies of living animals such as blood or muscle (Vander Zanden et al., 2015). While the amount of sea ice vs. pelagic phytoplankton-derived production is an important determinant with respect to consumer $\delta^{13}C$ values, other environmental factors are also significant.

The relative reliance of pelagic and benthic (bottom-associated) prey influences consumer tissue $\delta^{13}C$ values. Benthic habitats are characterized by higher $\delta^{13}C$ values relative to pelagic habitats (McConnaughey and McRoy, 1979); related to this, inshore areas tend to have higher $\delta^{13}C$ values than offshore areas and this is reflected in the $\delta^{13}C$ values of the consumers that forage in these respective areas (Cherel and Hobson, 2007; Hobson, 1993; Hobson et al., 1994). This pattern is driven by the decreasing strength of benthic-pelagic coupling as one moves further from shore (Kopp et al., 2015). Benthic-pelagic coupling is said to be 'tight' or 'strong' when a high proportion of the production in the photic zone is delivered to the benthos without being consumed by pelagic grazers (Hobson et al., 1995). Generally speaking, the percentage of organic matter produced in the photic zone that is delivered to the seabed is much higher in coastal marine environments relative to continental shelf and deep sea environments (Giordani et al., 2002). In some areas of the Arctic, such as the Bering-Chukchi Sea, benthic-pelagic coupling is especially strong and pelagic grazing is fairly insignificant, translating to high $\delta^{13}C$ values throughout the food web (Dunton et al., 1989).

Much like terrestrial producers, the $\delta^{13}C$ values of marine producers can be impacted by environmental variables such as temperature (Wiencke and Fischer, 1990), light intensity or day length (Burkhardt et al., 1999b; Cornelisen et al., 2007), external $[CO_2]$ (Burkhardt et al., 1999a, b; Laws et al., 1995), water turbulence (Osmond et al., 1981), algal cell size and geometry (Korb et al., 1996; Popp et al., 1998), and growth rate (Bidigare et al., 1997; Burkhardt et al., 1999a; Kopczyńska et al., 1995; Laws et al., 1995). Of these, only phytoplankton growth rate has been suggested as a mechanism driving variation in higher trophic level consumer tissue $\delta^{13}C$ values.

A strong relationship has been found between planktonic growth rate and plankton $\delta^{13}C$ values, with higher growth rates being associated with higher planktonic $\delta^{13}C$ values (Bidigare et al., 1997; Burkhardt et al., 1999a; Kopczyńska et al., 1995; Laws et al., 1995). Schell (2000, 2001) posited that declining primary productivity in the Gulf of Alaska/Bering Sea region was responsible for declining $\delta^{13}C$ values in bowhead whale baleen in the late 20th century, with average $\delta^{13}C$ values declining by 2.7‰ between 1947 and 1997; essentially, planktonic growth rates were higher and therefore primary productivity was also higher. Cullen et al. (2001), however, countered that the majority of this shift in $\delta^{13}C$ values

could be attributed to changes in the $\delta^{13}\text{C}$ value of the oceanic dissolved inorganic carbon pool driven by anthropogenic activities, specifically the combustion of ^{13}C -depleted fossil fuels and the resultant shift in atmospheric and oceanic CO_2 $\delta^{13}\text{C}$; Newsome et al. (2007) made similar arguments on the basis of northern fur seal tooth $\delta^{13}\text{C}$ values.

Consumer nitrogen isotopic compositions ($\delta^{15}\text{N}$) are influenced strongly by trophic position, as well as other environmental factors. Within a particular food web, there is a regular increase of 3–5‰ in $\delta^{15}\text{N}$ at each trophic level (Bocherens and Drucker, 2003; Minagawa and Wada, 1984), with 3.4‰ being the most commonly used value (Post, 2002; Vander Zanden and Rasmussen, 2001). Accordingly, changes in the trophic level of consumers over time can be examined by measuring the nitrogen isotopic compositions of their tissues (Becker and Beissinger, 2006; Emslie and Patterson, 2007; English et al., 2018; Wiley et al., 2013). A complication to such studies, however, is that the $\delta^{15}\text{N}$ value at the base of the food web (in nutrients and producers) can vary strongly according to nutrient availability and the dominant types of producers in the area (Altabet, 2006; Sigman et al., 2009) and will also vary over a range of temporal scales (Altabet et al., 1995, 1999; Meckler et al., 2011; Sherwood et al., 2011, 2014). Therefore, temporal variation in bulk tissue $\delta^{15}\text{N}$ from a single species could be driven by either a change in the feeding ecology of that species (a shift in trophic position) or by a change in $\delta^{15}\text{N}$ at the base of the food web. More robust interpretations can be made by measuring the $\delta^{15}\text{N}$ values of multiple contemporaneous taxa over the same span of time, with the expectation that a shift in $\delta^{15}\text{N}$ at the base of the food web should be reflected more-or-less equally among all taxa (Misarti et al., 2009).

Nitrogen isotope compositions at the base of marine food webs vary strongly geographically and a complex set of biologically-mediated reactions control the nitrogen isotopic composition of the different marine N pools (Altabet, 2006; Casciotti, 2016; Montoya, 2008; Sigman et al., 2009). Areas in which diazotrophic (nitrogen-fixing) bacteria are important producers (such as the western Gulf of Mexico) tend to have very low $\delta^{15}\text{N}$ values throughout the food web relative to areas in which phytoplankton are the dominant producers (Carpenter et al., 1997; Dorado et al., 2012; McClelland et al., 2003). Areas characterized by strong upwelling of nitrate and anoxic conditions, which favour denitrification (a process that enriches the residual nitrate in ^{15}N), tend to have high $\delta^{15}\text{N}$ values throughout the food web (Brandes et al., 1998; Cline and Kaplan, 1975; Voss et al., 2001). Areas with abundant diazotrophic bacteria and areas with significant denitrification represent the extremes of the range of variation observed in marine $\delta^{15}\text{N}$ (Montoya, 2008). Importantly, this variation is reflected in the tissues of consumers at higher trophic levels (Ruiz-Cooley et al., 2012; Ruiz-Cooley and Gerrodette, 2012; Wallace et al., 2006).

Within the context of paleoenvironmental studies, an advantage of isotopic measurements of the tissues of large predators is that they effectively integrate large amounts of short-term isotopic and hence environmental variation, effectively dampening to a significant degree 'noise' that may be present in other proxy records. In a terrestrial environment, Bump et al. (2007) demonstrated that the $\delta^{13}\text{C}$ values of wolf (*Canis lupus*) tissues better recorded recent (late 20th century) temporal variation in atmospheric CO_2 $\delta^{13}\text{C}$ values than did the tissues of herbivores (*Alces alces*) or plants (*Pinus flexilis*). These same principles also apply in marine ecosystems. Schaal et al. (2016) examined the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of marine producers through to predatory fishes in the Bay of Biscay along a depth gradient from 5 to 160 m. They found stronger correlations between depth and tissue $\delta^{13}\text{C}$ for carnivores than for primary consumers and particulate organic matter. Paleontological and archaeological deposits tend to be rich in terrestrial herbivores, but the abundance of terrestrial carnivores is typically much lower (e.g.,

Currant and Jacobi, 2001; Grayson, 1989; Harington, 2011). On the other hand, with only a few exceptions the vertebrate marine fauna that are abundant in archaeological deposits consist of animals that fed between the third and fifth trophic levels (see Pauly et al., 1998 for examples of marine mammal trophic levels). Marine mammals are therefore ideally suited to be faithful recorders of variation in the marine environment that can supplement other paleoenvironmental proxies.

5. Methods

5.1. Sites and samples

For stable isotope analysis, 759 ringed seal bones were sampled from 19 archaeological sites in the Central Canadian Arctic Archipelago dating between the Pre-Dorset and Thule periods (c. 4000–500 yr BP). The sites that were sampled are not evenly represented over time and can instead be broadly divided into four periods: (1) Pre-Dorset (4000–2800 yr BP, $n = 137$), (2) Early and Middle Dorset (2800–1500 yr BP, $n = 39$), (3) Late Dorset (1500–700 yr BP, $n = 111$), (4) Early Thule (700–500 yr BP, $n = 472$). Note that these temporal ranges do not necessarily represent the beginning and end points of any material culture tradition, but are specific to the material that was analyzed as part of this study.

Samples were selected according to the most abundant element in each discrete context; these discrete contexts were house or midden features at each of the sites.

For AMS (accelerator mass spectrometry) ^{14}C dating, terrestrial mammal bones (usually caribou or muskox) were selected from the same suite of sites where available. A few sites either lacked terrestrial mammal bone suitable for dating or were already sufficiently well dated and no new dates are reported here. A total of 48 bones were selected for AMS dating.

5.2. Sample preparation

Bone surfaces were cleaned by abrasion with an NSK Ultimate XL micromotor equipped with a diamond-tipped cutting wheel. Bone was demineralized in 0.5 M HCl at 4 °C. After demineralization, samples were rinsed to neutrality with Type I water. Any bone samples that were tan or brown in color were treated with 0.1 M NaOH for successive 30 min treatments under sonication at room temperature until the solution no longer changed color. The samples were again rinsed to neutrality with Type I water and then the insoluble collagen residue was solubilized in ~8 ml of 10^{-3} M HCl at 75 °C for 48 h. After heating, the resulting solution was filtered through a 5–8 µm filter to remove particulate matter and other insoluble residues and then filtered using a Microsep® 30 kDa molecular weight cut-off (MWCO) ultrafilter (Pall Corporation, Port Washington, NY) to remove low molecular weight compounds (Brown et al., 1988). The >30 kDa fraction was freeze-dried, and the collagen yield was calculated.

Samples prepared for AMS dating followed the same procedure but an Amicon® 30 kDa ultrafilter was used (Millipore, Darmstadt, Germany) and was cleaned following the procedure presented in Beaumont et al. (2010). Samples were AMS dated at the A.E. Lalonde Radiocarbon Laboratory at the University of Ottawa. Prior to dating, stable carbon and nitrogen isotopic compositions were determined as outlined below to confirm the terrestrial origin of the sample so as to eliminate the possibility of a misidentified polar bear (Gorlova et al., 2015).

5.3. Stable isotope analysis

Carbon and nitrogen isotopic and elemental compositions were

determined using an IsoPrime continuous flow isotope-ratio mass spectrometer (CF-IRMS) coupled to a Vario Micro elemental analyzer (Elementar, Hanau, Germany). Carbon and nitrogen isotopic compositions were calibrated relative to the VPDB and AIR scales, respectively, using a two-point calibration anchored by USGS40 (accepted $\delta^{13}\text{C}$ $-26.39 \pm 0.04\text{‰}$, $\delta^{15}\text{N}$ $-4.52 \pm 0.06\text{‰}$) and USGS41 (accepted $\delta^{13}\text{C}$ $+37.63 \pm 0.05\text{‰}$, $\delta^{15}\text{N}$ $+47.57 \pm 0.11\text{‰}$). Standard uncertainty was determined to be $\pm 0.20\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.25\text{‰}$ for $\delta^{15}\text{N}$ (Szpak et al., 2017b). Additional details on measurement calibration and analytical uncertainty are provided in the [Appendix](#).

5.4. Data treatment

All radiocarbon dates were calibrated using IntCal13 (Reimer et al., 2013). Ringed seal stable carbon and nitrogen isotopic compositions were compared between periods using Mann-Whitney U tests following a Shapiro-Wilk test for normality. Some contexts contained very few samples or could not be directly dated but could be clearly assigned to one of the four broad periods. For example, five ringed seal bones were sampled from three different contexts at Qijx-10, which were not specifically dated, although other features at this site have been dated. For these samples, the isotopic compositions were included in statistical comparisons among the four periods, but were excluded from summary tables and figures. These data are still included in the [Appendix](#) and a note indicates that the specific context from which they were sampled lacks a radiometric date.

Collagen integrity was monitored on the basis of collagen yields and elemental compositions (wt% C, wt% N, C:N ratios) (Ambrose, 1990; DeNiro, 1985; van Klinken, 1999). The yields that are reported represent the >30 kDa fraction of the collagen solution that did not pass through the ultrafilter and is not equivalent to the yields reported as reliable by Ambrose (1990) and van Klinken (1999). Ultrafiltration significantly reduces the collagen yields of even modern (Guiry et al., 2016) and extremely well-preserved archaeological bone (Szpak et al., 2017a) compared with methods that utilize all of the acid insoluble residue produced during the extraction.

5.5. Radiocarbon dates of naturally stranded bowheads

Summed radiocarbon probability distributions (SPDs) are statistical functions that are widely used as proxies of past population trends (Chaput and Gajewski, 2016; Crema et al., 2016; Timpson et al., 2014). Provided that the sample of radiocarbon dates contributing to an SPD are controlled to reduce biases in the density function—for example, by combining multiple dates from single events or individuals into a single date, and by removing dated materials with unknown offsets such as old wood or excessively wide standard deviations—then SPDs offer an opportunity for examining long-term cycles in relative population sizes. As radiocarbon samples have been collected for over 50 years, there is also an existing body of data than can be mined, compiled and reused that offers further opportunities for regional population history analysis (Bevan et al., 2017).

In this study, 522 samples of bone from naturally stranded bowhead whale from the CAA were collected from the dataset compiled by (Furze et al., 2014), which consists of directly dated bowheads from previously published studies. Each sample represents a unique individual.

The 522 samples were individually calibrated using the Marine13 Radiocarbon Age Calibration Curve (Reimer et al., 2013) with an offset of 170 ± 95 years. All dates were pooled into a single summed probability distribution using the function 'SPD' provided

in the R statistical package 'rcarbon' (Bevan and Crema, 2018). This produces a density curve illustrating the changing frequency of bowhead whale strandings from 12000 cal yrs BP to the present. As there are stochastic variations in the density curve over time arising from sampling effects and fluctuations in atmospheric carbon, a simulation of random strandings was used to create a 95 per cent confidence envelope to identify chronological periods where there are greater or fewer than expected strandings. To do so, a sample of 522 simulated mean radiocarbon dates from within the same observed time range were randomly generated by random selection with replacement from a uniform distribution, a standard deviation randomly selected from the vector of observed standard deviations, and finally the dates and standard deviations were then calibrated and pooled as with the observed data. This was repeated 1000 times. The upper and lower 97.5% confidence intervals were identified from the combined density function and added to the SPD. Peaks above the envelope represent periods in which there are greater-than-expected numbers of whale strandings at $p < 0.05$, and troughs below the envelope are periods where there are fewer-than-expected numbers of whale strandings. The R code used in this analysis is presented in the [supplementary material](#).

6. Results

6.1. Radiocarbon dates for archaeological sites

Radiocarbon dates for archaeological features associated with ringed seals analyzed in this study are presented in [Table 1](#). Additional published dates are included from PajS-13 (Savelle and Habu, 2004) and Qijx-10 (LeMoine et al., 2003), as well as previously unreported AMS dates from PajS-13 and PajS-4 that were not analyzed as part of this project (cited as Savelle and Dyke or Savelle and Habu, Unpublished Results in [Table 1](#)). Three dates produced anomalous results in that the radiocarbon ages do not correspond with the apparent cultural assignment of the sites. House 6 at PcJq-5 (Cape Garry), a Classic Thule occupation (McCartney, 1979; Rick, 1980), produced a date of 949 ± 24 ^{14}C yr BP, approximately 300 years older than the other dates obtained for that site ([Table 1](#)). Most likely this represents a portion of a Thule feature that was dug into a previously occupied Late Dorset dwelling, a relatively common occurrence in the Canadian Arctic (Dyke et al., 2019; Park, 1993). We have, therefore, excluded samples from this level, but since a second sample from House 6 produced a date consistent with a Classic Thule occupation, we have included ringed seal isotopic compositions from the other levels. The other anomalous dates come from two Late Dorset sites on Little Cornwallis Island, Qijx-10 (Tasiarulik) and Qijx-1 (Arvik). LeMoine et al. (2003) suggested a relatively brief occupation of Qijx-1 and reported two dates: 1580 ± 60 ^{14}C yr BP (Feature 49) and 1460 ± 60 ^{14}C yr BP (Feature 10). All of the new dates that we have produced are considerably younger ([Table 1](#)), including a date for Feature 10 of 980 ± 27 ^{14}C yr BP. Feature 16 produced a date that would represent a very recent Late Dorset occupation (604 ± 22 ^{14}C yr BP). This date is suspicious in the absence of additional dates, and we therefore suggest that an age closer to that of the other features (c. 1000 ^{14}C yr BP) is more reasonable for this feature. Similarly, Feature 84 at Qijx-10 produced dates of 1003 ± 28 and 610 ± 22 ^{14}C yr BP, while Feature 70 produced a date of 1007 ± 25 yr BP. These older dates are comparable to those reported by LeMoine et al. (2003) for this site, and we believe that they reflect its true age.

6.2. Stable isotope analysis

The stable carbon and nitrogen isotopic compositions of the ringed seals from each of the archaeological features sampled are

Table 1

List of radiocarbon dates for sites included in the analysis. All dates are on bone collagen.

Lab ID	Borden	Feature	Period	Species	¹⁴ C Age (¹⁴ C Years BP)	Calibrated Age, 2σ Range (cal Years BP)
UOC-1775	QkHn-13	Feature 1	Pre-Dorset	Caribou	3681 ± 27	3924–4091 (0.99)
UOC-1776	QkHn-13	Feature 1	Pre-Dorset	Caribou	3481 ± 26	4132–4137 (0.01)
UOC-1781	QkHn-13	Feature 4R	Pre-Dorset	Caribou/musk ox	3700 ± 29	3649–3659 (0.02)
UOC-1778	QkHn-13	Feature 14	Pre-Dorset	Caribou	3669 ± 28	3690–3834 (0.98)
UOC-1777	QkHn-13	Feature 14	Pre-Dorset	Caribou	3662 ± 28	3931–3943 (0.02)
UOC-1780	QkHn-13	Feature 15	Pre-Dorset	Caribou	3733 ± 26	3968–4098 (0.90)
UOC-1779	QkHn-13	Feature 15	Pre-Dorset	Caribou	3671 ± 31	4116–4146 (0.08)
UOC-1774	QkHn-13	Feature 4	Pre-Dorset	Musk ox	3471 ± 28	3911–4086
UOC-1772	QkHn-38		Pre-Dorset	Caribou	3653 ± 28	3903–4084
UOC-1773	QkHn-38	Midden	Pre-Dorset	Caribou	3637 ± 26	3985–4053 (0.39)
UOC-1782	QkHl-5		Pre-Dorset	Caribou	3600 ± 32	4060–4153 (0.61)
UOC-1785	RbJu-1	Feature 19	Pre-Dorset	Caribou/musk ox	3795 ± 28	3904–4088
UOC-1786	RbJu-1	Feature 21	Pre-Dorset	Caribou/musk ox	3730 ± 31	3645–3664 (0.07)
UOC-1787	RbJu-1	House 1	Pre-Dorset	Arctic fox	3708 ± 33	3686–3832 (0.93)
UOC-1784	RcJu-1	House 9	Pre-Dorset	Caribou	3260 ± 30	3892–4012 (0.73)
UOC-1771	QjLd-21		Early Dorset	Arctic fox	2528 ± 23	4028–4083 (0.27)
UOC-1768	QjLd-21	Locality 6	Early/Middle Dorset	Musk ox	1990 ± 24	3872–3994 (0.89)
UOC-1769	QjLd-21	Locality 7	Early/Middle Dorset	Musk ox	1984 ± 20	4038–4077 (0.11)
UOC-5914	QjLd-21		Early/Middle Dorset	Musk ox	1937 ± 41	3833–3983
UOC-1796	RbJu-1	Midden 7	Early Dorset	Arctic fox	2511 ± 27	4087–4249 (0.99)
UOC-1760	QjLa-3	Feature 2	Late Dorset	Arctic fox	975 ± 24	4274–4283 (0.01)
UOC-1759	QjLa-3	Feature 3	Late Dorset	Arctic fox	874 ± 26	3981–4154 (0.99)
UOC-1764	QjJx-1	Feature 3	Late Dorset	Arctic fox	939 ± 22	4210–4215 (0.01)
UOC-1765	QjJx-1	Feature 3	Late Dorset	Arctic fox	1048 ± 24	3933–3941 (0.01)
UOC-1761	QjJx-1	Feature 9	Late Dorset	Caribou/musk ox	972 ± 22	3970–4150 (0.99)
UOC-1762	QjJx-1	Feature 10	Late Dorset	Arctic fox	980 ± 27	3403–3430 (0.08)
UOC-1763	QjJx-1	Feature 16	Late Dorset	Arctic fox	604 ± 22	3442–3565 (0.92)
UOC-1758	QjJx-10	Feature 70	Late Dorset	Caribou	1007 ± 25	2498–2595 (0.46)
UOC-1756	QjJx-10	Feature 84	Late Dorset	Arctic fox	1003 ± 28	2613–2636 (0.14)
UOC-1757	QjJx-10	Feature 84	Late Dorset	Caribou	610 ± 22	2688–2742 (0.40)
TO-4535 ^a	QjJx-10	Feature 79	Late Dorset	Caribou	930 ± 120	1889–1992 (1.00)
TO-3737 ^a	QjJx-10	Feature 78	Late Dorset	Caribou	1550 ± 50	1889–1988 (1.00)
TO-4534 ^a	QjJx-10	Feature 91	Late Dorset	Caribou	920 ± 50	1743–1754 (0.01)
UOC-1766	QjLd-17		Late Dorset	Musk ox	879 ± 21	1810–1992 (0.99)
UOC-1767	QjLd-17		Late Dorset	Musk ox	775 ± 22	2490–2643 (0.73)
AA-53783 ^b	Pajs-13	House 1	Thule	Caribou	467 ± 44	2656–2666 (0.01)
TKa-16251 ^c	Pajs-13	House 1	Thule	Caribou	594 ± 18	2677–2738 (0.26)
TKa-16253 ^c	Pajs-13	House 2	Thule	Caribou	495 ± 20	796–874 (0.54)
TKa-16254 ^c	Pajs-13	House 2	Thule	Caribou	489 ± 20	895–935 (0.46)

Table 1 (continued)

Lab ID	Borden	Feature	Period	Species	¹⁴ C Age (¹⁴ C Years BP)	Calibrated Age, 2σ Range (cal Years BP)
TKa-16255 ^c	PaJs-13	House 2	Thule	Caribou	499 ± 19	510–539
TKa-16256 ^c	PaJs-13	House 2	Thule	Caribou	473 ± 18	503–531
AA-53794 ^b	PaJs-13	House 3	Thule	Caribou	582 ± 46	527–655
AA-53792 ^b	PaJs-13	House 3	Thule	Caribou	613 ± 46	540–663
TKa-16257 ^c	PaJs-13	House 4	Thule	Caribou	601 ± 19	546–569 (0.23) 582–649 (0.78)
TKa-16258 ^c	PaJs-13	House 4	Thule	Caribou	633 ± 18	557–604 (0.60) 627–660 (0.40)
AA-53789 ^b	PaJs-13	House 4	Thule	Caribou	620 ± 66	527–675
AA-53785 ^b	PaJs-13	House 4	Thule	Caribou	419 ± 42	319–380 (0.20) 387–391 (0.01) 427–530 (0.80)
AA-53793 ^b	PaJs-13	House 5	Thule	Caribou	761 ± 47	653–782
AA-53791 ^b	PaJs-13	House 5	Thule	Caribou	601 ± 51	533–662
TKa-16259 ^c	PaJs-13	House 5	Thule	Caribou	602 ± 18	547–568 (0.22) 582–649 (0.78)
TKa-16260 ^c	PaJs-13	House 5	Thule	Caribou	554 ± 19	527–559 (0.62) 600–630 (0.38)
TKa-16261 ^c	PaJs-13	House 5	Thule	Caribou	617 ± 20	552–613 (0.61) 619–655 (0.39)
TKa-16262 ^c	PaJs-13	House 5	Thule	Caribou	531 ± 19	517–554 (0.94) 610–621 (0.06)
UOC-5920	PcJq-5	House 5	Thule	Caribou	685 ± 41	556–606 (0.38) 625–690 (0.62)
UOC-1809	PcJq-5	House 6	Thule	Caribou	949 ± 24	796–886 (0.74) 891–925 (0.26)
UOC-1810	PcJq-5	House 6	Thule	Caribou	623 ± 24	552–612 (0.61) 619–658 (0.39)
UOC-1803	PcJq-5	House 7	Thule	Caribou	668 ± 23	562–593 (0.44) 637–672 (0.56)
UOC-1801	PcJq-5	House 7	Thule	Caribou	511 ± 24	508–550 (1.00)
UOC-1811	PeJr-1	House 1	Thule	Caribou	482 ± 24	503–537 (1.00)
UOC-1802	PeJr-1	House 5	Thule	Caribou	575 ± 22	535–564 (0.36) 589–641 (0.64)
UOC-1788	QkLi-1	Site 10	Thule	Caribou/musk ox	628 ± 24	553–611 (0.60) 621–661 (0.40)
UOC-1790	RbJr-1	House 8	Thule	Caribou	667 ± 25	561–596 (0.45) 634–673 (0.55)
UOC-1789	RbJr-1	254	Thule	Goose	576 ± 23	535–564 (0.35) 588–642 (0.65)
UOC-1793	RbJr-1	House 4	Thule	Caribou	529 ± 25	513–556 (0.88) 606–625 (0.12)
UOC-1791	RbJr-1	House 2	Thule	Caribou	501 ± 34	501–555 (0.96) 609–622 (0.04)
UOC-1792	RbJr-1	House 1	Thule	Caribou	491 ± 27	504–542 (1.00)
UOC-1795	RbJr-4	House 1	Thule	Caribou	540 ± 26	516–559 (0.74) 600–631 (0.27)
UOC-1794	RbJr-4		Thule	Caribou	520 ± 24	510–554 (0.96) 610–620 (0.04)
UCIAMS-42220 ^d	PaJs-4		Thule	Caribou	610 ± 15	551–570 (0.20) 580–651 (0.80)
UCIAMS-42221 ^d	PaJs-4		Thule	Caribou	390 ± 15	335–349 (0.10) 440–443 (0.01) 451–504 (0.89)
UCIAMS-44020 ^d	PaJs-4		Thule	Caribou	365 ± 25	318–394 (0.44) 425–499 (0.56)

^a LeMoine et al. (2003).^b Saville and Habu (2004).^c Saville and Habu (Unpublished Results).^d Saville and Dyke (Unpublished Results).

presented in Figs. 3 and 4. The results are summarized by context in Table 2 and all individual data are presented in Table S4. Eight out of 759 samples analyzed produced atomic C:N ratios that were >3.60 and were excluded from further analyses; the results are still presented in Table S4. At the level of individual features the mean ringed seal bone collagen $\delta^{13}\text{C}$ values increased steadily between the earliest sites dating to around 4000 yr BP through to the Late Dorset sites around 850 yr BP although the representation of sites dating between 3450 and 950 yr BP is limited. There were significant differences in the ringed seal $\delta^{13}\text{C}$ values among the four

periods (Table 3). The Early Dorset ringed seal $\delta^{13}\text{C}$ values were significantly higher than the Pre-Dorset ringed seals ($U = 1,550$, $p < 0.001$) and the Late Dorset ringed seal $\delta^{13}\text{C}$ values were significantly higher than the Early Dorset ringed seal $\delta^{13}\text{C}$ values ($U = 126$, $p < 0.001$). Focusing specifically on Late Dorset and Thule occupations, the ringed seals from the Thule sites (700–500 yr BP) were characterized by much lower $\delta^{13}\text{C}$ values than ringed seals from the slightly earlier Late Dorset sites; this difference was statistically significant ($U = 19,984$, $p < 0.001$). The Thule ringed seals were also characterized by a greater range of variation in $\delta^{13}\text{C}$

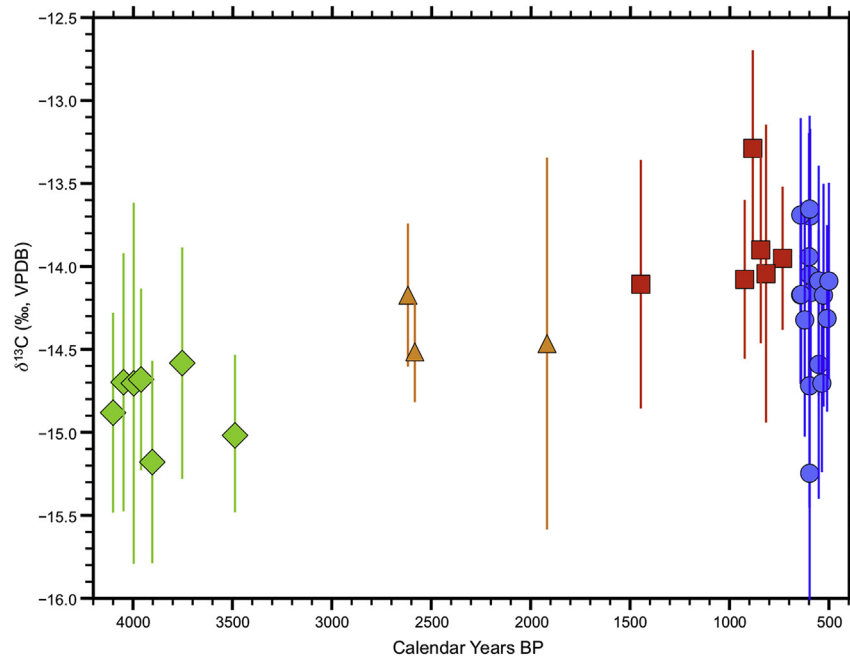


Fig. 3. Ringed seal carbon isotopic compositions through time. Each symbol represents the mean, errors bars represent standard deviations: diamonds (Pre-Dorset), triangles (Early and Middle Dorset), squares (Late Dorset), circles (Thule).

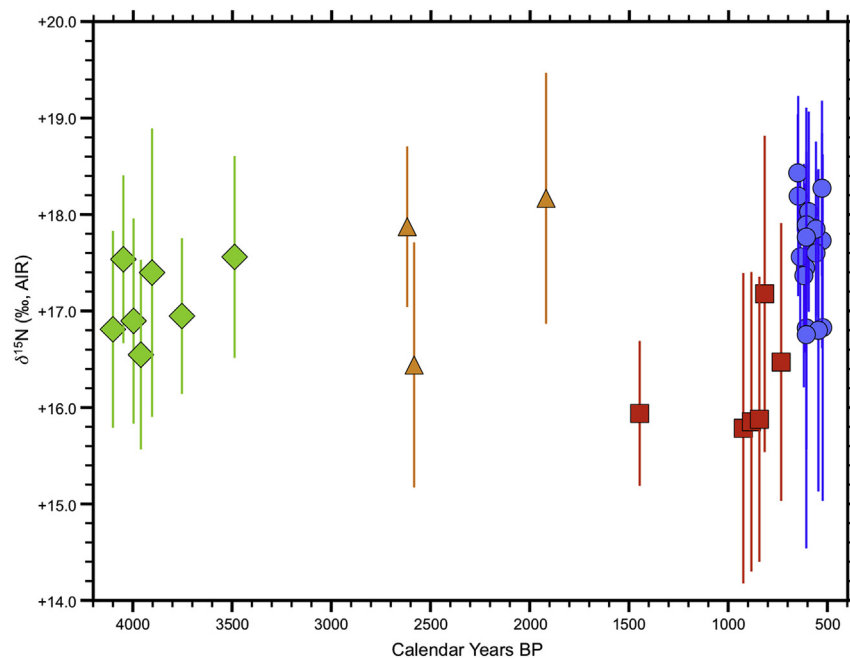


Fig. 4. Ringed seal nitrogen isotopic compositions through time. Each symbol represents the mean, errors bars represent standard deviations: diamonds (Pre-Dorset), triangles (Early and Middle Dorset), squares (Late Dorset), circles (Thule).

values than the Late Dorset ringed seals (Fig. 3), although there are more discrete site features and at least twice as many individual samples associated with Thule occupations relative to any other period.

Unlike $\delta^{13}\text{C}$, there were no clear patterns in the ringed seal $\delta^{15}\text{N}$ values prior to 950 yr BP, although there were significant differences among some of the four time periods (Table 4). There was no significant difference in the $\delta^{15}\text{N}$ values between the Pre-Dorset

and Early Dorset ringed seals ($U = 2,322$, $p = 0.24$), but the Late Dorset ringed seals had significantly lower $\delta^{15}\text{N}$ values than the Pre-Dorset ($U = 5,029$, $p < 0.001$) and Early Dorset ($U = 1,291$, $p < 0.001$) ringed seals. As with the $\delta^{13}\text{C}$ values, there was a clear distinction between the Late Dorset and Thule periods. Ringed seals from the Late Dorset sites had significantly lower $\delta^{15}\text{N}$ values than ringed seals from the Thule sites ($U = 11,441$, $p < 0.001$).

Table 2Summarized ringed seal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm 1 σ) for the contexts examined.

Period	Site	Feature	2 σ Range (yrs BP)	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Pre-Dorset	QkHn-13	F1, F4	4137–3649	29	−14.58 \pm 0.70	+16.95 \pm 0.82
Pre-Dorset	QkHn-13	F14	4086–3903	7	−14.70 \pm 1.09	+16.90 \pm 1.08
Pre-Dorset	QkHn-13	F15, F4R	4153–3904	16	−14.69 \pm 0.78	+17.54 \pm 0.87
Pre-Dorset	QkHn-38		4083–3872	15	−14.68 \pm 0.55	+16.55 \pm 0.99
Pre-Dorset	RbjU-1		4087–3933	42	−14.87 \pm 0.60	+16.81 \pm 1.02
Pre-Dorset	RcjU-1		3430–3403	13	−15.01 \pm 0.47	+17.56 \pm 1.06
Pre-Dorset	QkHl-5		3983–3833	14	−15.17 \pm 0.61	+17.39 \pm 1.51
E/M Dorset	QjLd-21		1992–1810	16	−14.46 \pm 1.12	+18.17 \pm 1.31
E/M Dorset	QjLl-21		2742–2498	7	−14.17 \pm 0.43	+17.88 \pm 0.83
E/M Dorset	RbjU-1	F7	2738–2490	16	−14.51 \pm 0.30	+16.44 \pm 1.28
Late Dorset	QjLa-3		935–727	12	−14.04 \pm 0.90	+17.18 \pm 1.65
Late Dorset	QjJx-1		1047–796	15	−13.29 \pm 0.59	+15.85 \pm 1.57
Late Dorset	QjJx-10	F70, F84	967–800	29	−14.08 \pm 0.48	+15.78 \pm 1.62
Late Dorset	QjJx-10	F78	1546–1344	3	−14.11 \pm 0.75	+15.95 \pm 0.75
Late Dorset	QjJx-10	F79/91	1082–658	7	−13.90 \pm 0.56	+15.87 \pm 1.49
Late Dorset	QjLd-17		902–675	39	−13.95 \pm 0.43	+16.46 \pm 1.46
Thule	PaJs-13	H1	645–334	24	−14.32 \pm 0.70	+17.55 \pm 0.85
Thule	PaJs-13	H2	539–510	57	−14.08 \pm 0.69	+17.60 \pm 0.85
Thule	PaJs-13	H3	663–527	60	−14.05 \pm 0.72	+17.89 \pm 0.76
Thule	PaJs-13	H4	675–319	69	−14.59 \pm 0.81	+17.84 \pm 0.90
Thule	PaJs-13	H5	782–517	20	−14.16 \pm 0.49	+18.05 \pm 0.77
Thule	PaJs-4		651–318	22	−14.19 \pm 0.54	+17.76 \pm 0.76
Thule	PcjQ-5	H5	690–556	8	−13.69 \pm 0.58	+18.42 \pm 0.61
Thule	PcjQ-5	H6	658–552	38	−13.70 \pm 0.53	+17.44 \pm 0.88
Thule	PcjQ-5	H7	672–562	11	−14.17 \pm 0.56	+18.18 \pm 1.04
Thule	PeJr-1	H1	537–503	6	−14.09 \pm 0.59	+18.26 \pm 0.91
Thule	PeJr-1	H5	641–535	7	−13.66 \pm 0.56	+17.36 \pm 1.16
Thule	QjJx-1	F16	651–546	6	−13.93 \pm 0.75	+16.82 \pm 2.28
Thule	QkLi-1		661–553	5	−14.71 \pm 0.74	+17.77 \pm 1.29
Thule	Rbjr-1	254	642–535	15	−15.25 \pm 0.80	+16.77 \pm 1.20
Thule	Rbjr-1	H1, 2, 4	625–501	27	−14.31 \pm 0.56	+17.73 \pm 1.11
Thule	Rbjr-1	H8	673–561	10	−14.17 \pm 0.67	+16.82 \pm 1.80
Thule	Rbjr-4		631–510	22	−14.70 \pm 0.53	+16.80 \pm 1.67
Thule	PcjQ-5	H21	Thule ^a	7	−14.04 \pm 0.31	+17.53 \pm 0.45
Thule	Rbjr-1	H10	Thule ^a	7	−14.47 \pm 1.26	+16.52 \pm 0.81
Thule	Rbjr-1	H9	Thule ^a	9	−14.05 \pm 0.67	+17.22 \pm 0.85
Thule	RbjU-1	H4	Thule ^a	11	−14.08 \pm 0.44	+17.01 \pm 1.00
Thule	RbjU-1	H5	Thule ^a	5	−14.09 \pm 0.32	+16.83 \pm 0.94

^a Individual feature has not been directly dated. These samples were included in the statistical comparisons among periods but these features are not presented in Figs. 3 and 4.

Table 3

Results of the statistical comparisons of the ringed seal stable carbon isotopic compositions between the four periods. Statistically significant differences are indicated in boldface.

$\delta^{13}\text{C}$	Early/Middle Dorset	Late Dorset	Thule
Pre-Dorset	$U=1550, p < 0.001$	$U=2388, p < 0.001$	$U=16697, p < 0.001$
Early/Middle Dorset	—	$U=126, p < 0.001$	$U=7558, p=0.084$
Late Dorset	—	—	$U=19984, p < 0.001$

Table 4

Results of the statistical comparisons of the ringed seal stable nitrogen isotopic compositions between the four periods. Statistically significant differences are indicated in boldface.

$\delta^{15}\text{N}$	Early/Middle Dorset	Late Dorset	Thule
Pre-Dorset	$U=2322, p=0.24$	$U=5029, p < 0.001$	$U=21108, p < 0.001$
Early/Middle Dorset	—	$U=1291, p < 0.001$	$U=7984, p=0.22$
Late Dorset	—	—	$U=11441, p < 0.001$

7. Discussion

7.1. Temporal trends in ringed seal stable carbon isotope compositions

Ringed seal bone collagen carbon isotopic compositions increased over time between the earliest Pre-Dorset through to the Late Dorset period. The Thule ringed seal bone collagen carbon

isotopic compositions were far more variable, but were on average lower than those from Late Dorset contexts. There are two primary mechanisms that have likely driven this increase into the Late Dorset period. First, the higher ringed seal $\delta^{13}\text{C}$ values may signal an increase in the relative proportion of carbon derived from ice-associated algae relative to phytoplankton because the former have consistently higher $\delta^{13}\text{C}$ values than the latter. A second related explanation involves increased foraging on benthic relative

to pelagic prey during those periods where ringed seal $\delta^{13}\text{C}$ values were highest. Muscle samples reflecting recent dietary intake from a modern Hudson Bay ringed seal population were characterized by significantly lower $\delta^{13}\text{C}$ values during the summer open water period (August–December) relative to the ice covered period (January–May) (Young and Ferguson, 2013). It is entirely possible that both of these factors (relative use of benthic and pelagic prey, relative importance of sympagic and pelagic production) contributed to the variation observed in ringed seal bone collagen $\delta^{13}\text{C}$ values as productivity of pelagic prey may increase with decreased sea ice extent and regional warming (Ershova et al., 2015). Ringed seals generally forage in more pelagic environments further from the shore or ice edge during the open water season (when the contribution of sympagic production would be minimal) and when sea ice is extensive, tend to rely to a greater extent on benthic resources (Young and Ferguson, 2013). Therefore, both explanations are causally tied to sea ice extent.

The range of variation observed among the ringed seals from different time periods is relatively small, but this is to be expected. Large-scale shifts in the relative importance of sympagic production or the strength of sympagic-pelagic coupling should be reflected as only relatively subtle shifts in consumer $\delta^{13}\text{C}$ values for two reasons. First, the difference between sea ice algae and phytoplankton $\delta^{13}\text{C}$ values (c. 5–10‰) are smaller than, for example, the difference between C_3 and C_4 plants (c. 14‰). Second, unlike C_3 and C_4 plants, for which it is theoretically possible in terrestrial environments to be reliant on 100% of either source, this is not possible for marine fauna in the Arctic. With the exception of a few highly specializing meiofauna, which are not major contributors of biomass to higher trophic levels, a 100% contribution of sympagic carbon for a given taxon, such as ringed seal, is unrealistic. Therefore, we might expect a significant shift in the relative contribution of sympagic production to be from 25% to 10%. Assuming that sea ice algae and phytoplankton have $\delta^{13}\text{C}$ values that are 10‰ apart (likely an overestimate), this would mean that a 15% change in the contribution of sea ice algae would result in a change of 1.5‰ in the consumer $\delta^{13}\text{C}$ value (following Schwarcz, 1991). This also assumes that no other variables (e.g., benthic vs. pelagic foraging) influence the consumer $\delta^{13}\text{C}$ value. The important point here is that small changes in ringed seal $\delta^{13}\text{C}$ values are consistent with reasonably large shifts in the productivity of sea ice. On the basis of the ringed seal carbon isotopic compositions, we propose increasing productivity derived from sympagic relative to pelagic sources from the earliest Pre-Dorset through to the Late Dorset period, followed by a sudden overall decrease in sympagic production coincident with the arrival of the Thule. Because of the lack of Dorset material dating between 2000 and 1000 yrs BP, we cannot say that the seemingly linear trend existed as such in this undersampled interval. On the basis of lipid biomarkers, Vare et al. (2009) suggest that the CAA was characterized by highly variable sea ice extent during this period on relatively short timescales (see also Belt et al., 2010), with no overarching temporal trend. It is therefore entirely possible that these highly variable conditions existed and would have obscured the apparent trends in our data but appropriate faunal materials are not available to sample dating from this period.

7.2. Temporal trends in ringed seal stable nitrogen isotope compositions

The clearest temporal pattern in the ringed seal nitrogen isotopic compositions is the distinction between the Late Dorset and Thule material with Thule ringed seals having significantly higher $\delta^{15}\text{N}$ values than Late Dorset ringed seals (Fig. 4). Unlike $\delta^{13}\text{C}$ there is no consistent differentiation of sea ice algae and phytoplankton

with respect to $\delta^{15}\text{N}$ so the shift in ringed seal $\delta^{15}\text{N}$ cannot be attributed to a change in the contribution of sympagic and pelagic production. It is not likely that a shift in the importance of phytoplankton reliant on nitrate vs. diazotrophic bacteria is responsible for this shift as N_2 -fixing cyanobacteria, which are the dominant N_2 -fixers in the oceans globally (Carpenter and Capone, 2008), but are scarce in Arctic seas (Tremblay et al., 2009). For the present study area N_2 -fixation rates in Lancaster Sound are extremely low (Blais et al., 2012). It is, therefore, more likely that a change in the types of prey consumed by ringed seals are responsible for the higher $\delta^{15}\text{N}$ values observed in Thule relative to Late Dorset ringed seals.

Aside from Arctic cod, zooplankton – amphipods (*Themisto libellula*) and mysids (*Mysis oculata*) – are important prey items for the ringed seal in the study area (Holst et al., 2001; McLaren, 1958). In their study of the North Water Polynya, Hobson et al. (2002) found the following average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the previously discussed ringed seal prey items: $-20.3 \pm 0.1\text{‰}$, $+10.4 \pm 0.1\text{‰}$ (*Mysis oculata*), $-20.4 \pm 0.1\text{‰}$, $+9.7 \pm 0.1\text{‰}$ (*Themisto libellula*), $-19.3 \pm 0.1\text{‰}$, $+14.0 \pm 0.2$ (Arctic cod, adult); comparable differences between species were reported by Yurkowski et al. (2016) for Resolute Bay. Therefore, a shift from lower (amphipods and mysids) to higher (Arctic cod) trophic level prey would be consistent with the observed increase in $\delta^{15}\text{N}$ values for the Thule relative to the Late Dorset ringed seals, but the decline in $\delta^{13}\text{C}$ values is inconsistent with this explanation as Arctic cod have higher tissue $\delta^{13}\text{C}$ values than these lower trophic level zooplankton taxa (Hobson et al., 2002; Matley et al., 2015; Yurkowski et al., 2016). Other higher trophic level prey such as sculpins (e.g., *Myoxocephalus scorpius*) could have figured as important prey as they have relatively high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (McMeans et al., 2013) but there is no evidence to suggest that they are or have been quantitatively significant prey items for ringed seals.

Arctic cod undergo significant ontogenetic changes in diet and habitat use and consequently in tissue isotopic compositions, a common pattern among fish (e.g., Fontoura et al., 2015; Graham et al., 2007; Post, 2003). In particular juvenile and larval Arctic cod are more closely associated with sympagic habitats, while adults tend to be associated with more pelagic habitats (Hop and Gjøsaeter, 2013; Kohlbach et al., 2017). This ontogenetic variation results in smaller individuals having higher $\delta^{13}\text{C}$ values and lower $\delta^{15}\text{N}$ values than larger individuals (Matley et al., 2013). Therefore, a shift from predominantly younger, ice-associated Arctic cod in the Late Dorset ringed seals to predominantly older, pelagic Arctic cod in the Thule ringed seals would be consistent with the observed trends in both the ringed seal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

7.3. Paleoenvironmental Implications

Isotopic records derived from archaeological faunal remains are not directly analogous to those derived from more traditional paleoclimatic sources such as marine sediment cores. Because the material is derived from animals that were hunted by humans, these materials have been passed through a so-called ‘cultural filter’ (Reed and Braidwood, 1960) and do not represent a random sampling of faunal isotopic compositions at a given point in time. Instead, these records represent a more dynamic series of interactions between people and their environment, specifically the animals that they actually interacted with through hunting. The most significant negative implication of this cultural filter is that the temporal distribution of samples is prone to be very uneven, particularly in environments where human occupation is sporadic. This is certainly true in the Canadian Arctic, as demonstrated by the demographic oscillations between 4000 and 1000 yr BP (e.g.

Savelle and Dyke, 2009; Savelle and Dyke, 2014). Because entire regions may have been abandoned at the extreme points of climatic oscillations, those times will not be captured in the kind of data that are presented in this study. Therefore, it would not be accurate to suggest that because the ringed seal $\delta^{13}\text{C}$ values are highest during the Late Dorset period that this implies this is the time at which ice algal productivity was highest between 4000 and 500 years BP. The unevenness of human occupation over millennia necessarily precludes such interpretations, but relative comparisons between periods of human occupation for which data exist or can be collected are reasonable.

The temporal resolution of these archaeological data is coarse, necessarily limited by the uncertainty of radiocarbon determinations at best. It is, therefore, important to contextualize these data with respect to other paleoclimatic proxies, which are not hampered by the bias of the cultural filter and typically have much finer resolution, but have other limitations, such as not providing insight into dynamics at or near the top of the food web or difficulties modeling sedimentation rates and relating depth to age.

The pattern of increasing ringed seal $\delta^{13}\text{C}$ values between the pre-Dorset and Late Dorset periods suggests increasing contributions of sea ice-derived algae over time. These data are consistent with other paleoclimatic proxy data demonstrating decreasing temperatures through the Holocene (Fig. 5). Decreasing Arctic temperatures through the Holocene have been widely observed (Briner et al., 2006, 2016; Fisher et al., 1983, 1995, 1998; Francis et al., 2006; Miller et al., 2010b), although the timing of this cooling and the period of peak warmth (Holocene Thermal Maximum) vary across space (Gajewski, 2015; Kaufman et al., 2004).

The shift in ringed seal $\delta^{13}\text{C}$ values at the Late Dorset-Thule transition, which we have interpreted as being driven by warmer temperatures and a decrease in sea ice productivity, is also evident in the Penny Ice Cap $\delta^{18}\text{O}$ record and the magnetic susceptibility record at Big Round Lake (both from Baffin Island). Much of the short-term variation recorded in high resolution records, such as those derived from ice cores, is unlikely to be observed in the isotopic compositions of mammals recovered from archaeological contexts. The slow turnover rate of bone collagen, the inclusion of animals hunted over a period of years to decades when sampling different contexts, and the uncertainty in the radiocarbon dates all serve to obscure this variation.

Our interpretation of increased productivity derived from sea ice algae between the Pre-Dorset and Late Dorset periods (c. 4000–1000 yr BP) is consistent with Vare et al.'s (2009) interpretation of the abundance of the sea ice algal biomarker IP₂₅ (Belt and Müller, 2013) in a sediment core spanning 10,000–400 yr BP in Barrow Strait (Fig. 6). One important difference, however, is that sea ice productivity appears to peak around 2500 yr BP in the data presented by Vare et al. (2009) whereas our data suggest that this peak occurs later, around 750 yr BP. Importantly, we do not have any ringed seal $\delta^{13}\text{C}$ data from the same period as the IP₂₅ peak observed by Vare et al. and this may be because the region was characterized by ice conditions that were too severe for human occupation at this time, precluding the formation of archaeological deposits. Conversely, there is no evidence of a period of pronounced cooling during this period relative to the rest of the Holocene (Fig. 5) and the minimum abundance of bowheads in the central Canadian Arctic (a proxy for sea ice extent) does not occur until after 1500 yr BP (Fig. 6). Several other studies have indicated a pattern of increasing sea ice extent through the middle Holocene in the CAA and the Arctic Ocean more generally based on a variety of proxies (Belt et al., 2010; Cronin et al., 2010; Dyke et al., 1996; Leduc et al., 2010). This pattern does not hold throughout the entire Arctic, with some areas, such as the Bering/Chukchi Sea region

experiencing a decrease in sea ice extent over the same period, with large millennial-scale oscillations (de Vernal et al., 2005).

Given that the earliest ringed seals (c. 4000 yr BP) have the lowest $\delta^{13}\text{C}$ values of any of the sites analyzed suggests that at this time the CAA experienced the lowest amount of sympagic productivity reaching higher trophic levels over the period studied. This scenario is consistent with the extensive study of naturally-stranded Holocene bowhead whales by Dyke et al. (1996) who found that from 5000 to 3000 ^{14}C yr BP bowheads had a wider geographic distribution than at present, moving into the channels of the central CAA. This range extension would only be possible if sea ice did not exclude the whales from this region, which is the case today. This peak in bowhead abundance is clearly visible in the summed probability distributions of ^{14}C dates from naturally-stranded whales (Fig. 6). Aside from the trend towards increasing $\delta^{13}\text{C}$ values between 4000 and 1000 yr BP, the most salient trend in the ringed seal isotopic data exists between the Late Dorset and Thule ringed seals.

As discussed in the following section, climatic variation has often been discussed in the context of the arrival of the Thule in the Canadian Arctic (Finkelstein et al., 2009). Our data suggest conditions of greater open water and lower relative contributions of sympagic production during the Thule relative to the Late Dorset periods (Fig. 3). Several high-resolution paleoclimate proxies provide evidence consistent with this scenario. Although the lipid biomarker data presented by Vare et al. (2009) do not show any marked differences in IP₂₅ flux around the time of the Thule-Dorset transition, they do note a short term decrease in spring sea ice extent in Barrow Strait between 1200 and 800 yr BP, which immediately precedes the Dorset-Thule temporal boundary. Varved sediments from Donard Lake on Baffin Island indicate extended cold periods lasting c. 50 years at 950 and 800 yr BP (Moore et al., 2001), corresponding to the terminal Late Dorset contexts. Furthermore, they demonstrate an extended period of warmth after 730 yr BP, corresponding to the arrival of the Thule. This extended warm period is also observed in other paleoclimatic records from the northern hemisphere (Cronin et al., 2003; Macias Fauria et al., 2010; Mann et al., 2008; Massé et al., 2008; McGovern, 1991).

The ringed seal $\delta^{13}\text{C}$ values were more variable in the Late Dorset and especially the Thule periods than they were in the earliest material (Fig. 3). While this may be, to some extent, an artifact of sample size, it may also be driven by higher short-term variation in sea ice productivity. Additional analyses focused on the periods preceding and succeeding the Thule occupation would help to resolve this issue.

While there are some similarities among the three datasets compared in Fig. 6 such as a broad trend of increasing sea ice productivity over time, there are clearly some inconsistencies. Some discordance between these proxies is to be expected and indeed, Pieńkowski et al. (2017) highlighted significant differences in sea ice reconstructions based on lipid biomarkers and dinocysts from within the same core in the Coronation Gulf region of the western Canadian Arctic. Nonetheless, the data derived from archaeological marine mammal tissues can still provide data regarding environmental conditions from the perspective of the top of the food web, which cannot be easily obtained from other proxies. Given that every proxy used for understanding past environments is characterized by its own set of limitations (Birks and Birks, 2006; Birks et al., 2010), we concur with the conclusions of Pieńkowski et al. (2017) that a single 'best' proxy is unlikely to exist, and therefore a multiproxy approach will provide a more in-depth understanding of environmental changes as they relate to past sea ice conditions.

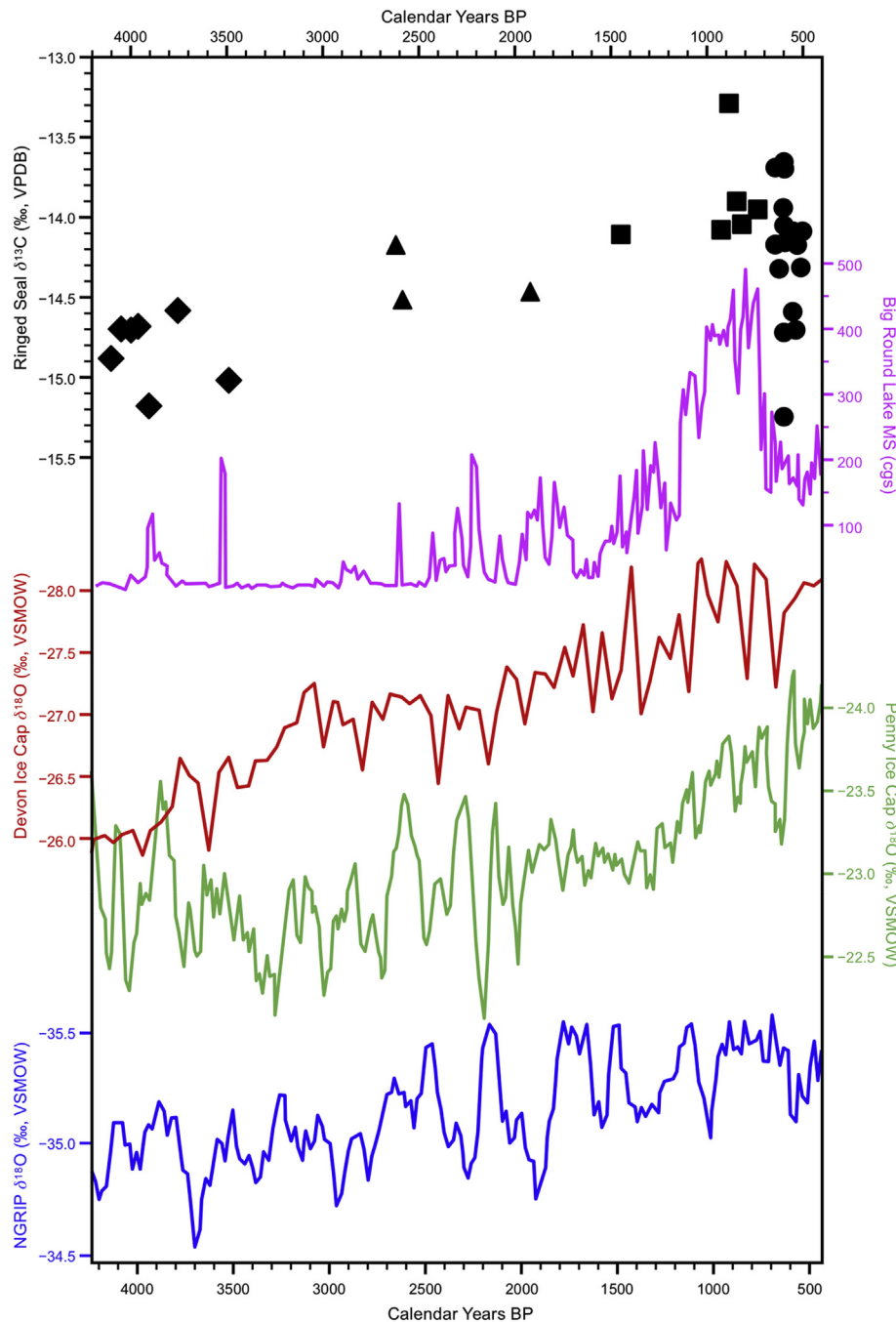


Fig. 5. Comparison of ringed seal $\delta^{13}\text{C}$ values to other paleoclimate proxy data. Each black symbol represents the mean for a particular feature with the error bars being omitted for the sake of clarity (but see Fig. 3); different symbols reflect the four different cultural periods outlined in the text. Data were compiled from the results summarized by Sundqvist et al. (2014), with the original sources of the data being: Big Round Lake (northeast Baffin Island) magnetic susceptibility (Thomas et al., 2010), Devon Ice Cap $\delta^{18}\text{O}$ (Fisher et al., 1983), Penny Ice Cap $\delta^{18}\text{O}$ (Fisher et al., 1998), North Greenland Ice Core Project (NGRIP) $\delta^{18}\text{O}$ (North Greenland Ice Core Project Members, 2004; Vinther et al., 2006). The Penny Ice Cap and NGRIP $\delta^{18}\text{O}$ records depicted represent five point running means.

7.4. Archaeological implications

The ringed seals from the earliest pre-Dorset contexts had the lowest $\delta^{13}\text{C}$ values, with increasing $\delta^{13}\text{C}$ values in the subsequent Middle and Late Dorset periods (Fig. 3). As discussed previously this trend is consistent with other proxies indicating decreasing temperatures and increasing sea ice extent after the Holocene thermal maximum c. 5000 yr BP. Based on extensive radiocarbon dating of archaeological features on raised beaches, Saville and Dyke have

demonstrated a series of demographic shifts (boom and bust cycles) in human settlement throughout much of the Canadian Arctic (Dyke and Saville, 2009; Dyke et al., 2011; Saville and Dyke, 2002, 2009; 2014; Saville et al., 2012). Notably, the height of the peaks associated with the booms (represented by the number of individual dwelling features) declines over time, with the highest peaks consistent with the earliest pre Dorset occupation, and the lowest peaks consistent with the Late Dorset occupation. A correlation therefore appears to exist between the size of human populations

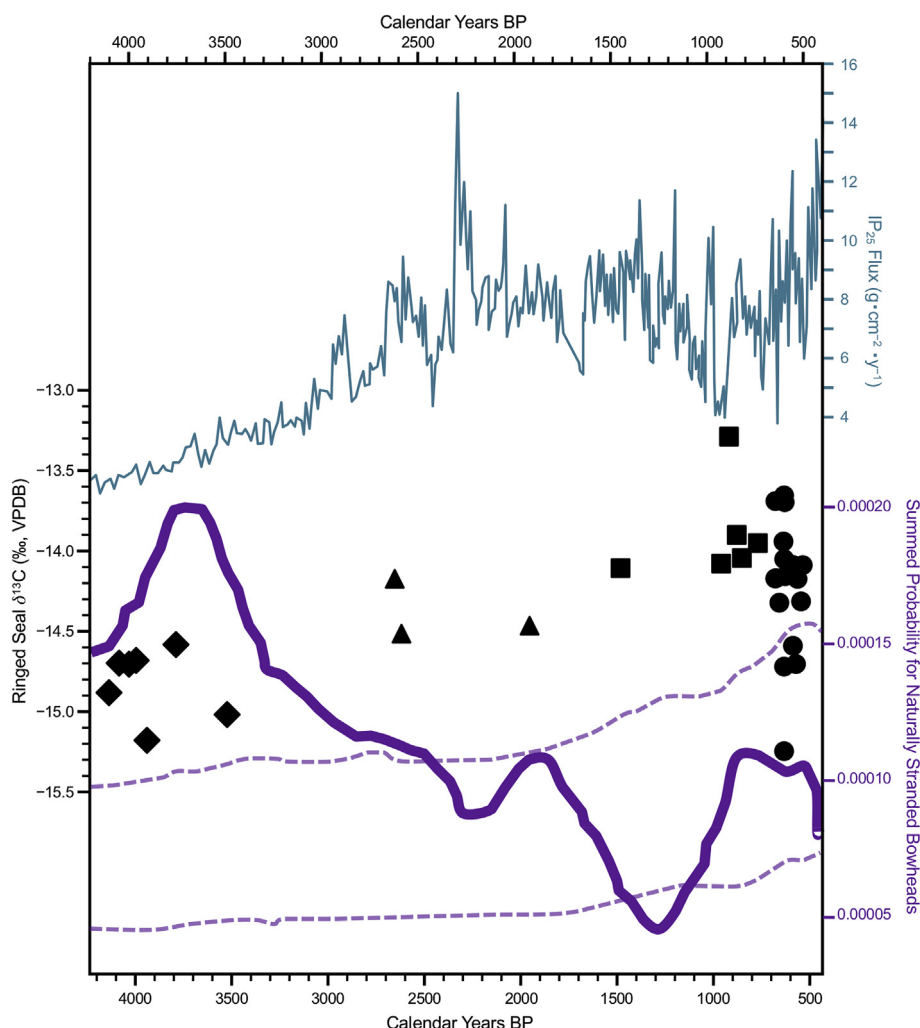


Fig. 6. Comparison of mean ringed seal $\delta^{13}\text{C}$ values for dated archaeological features (solid symbols), IP_{25} flux from a core in Barrow Strait, and a summed probability distribution based on naturally stranded ^{14}C -dated bowhead whales.

in the CAA and sea ice conditions, with smaller populations being associated with colder conditions and increased sea ice coverage as reflected in the ringed seal $\delta^{13}\text{C}$ values (Fig. 3). However, this begs the question of why this apparent correlation should exist, since it would be expected that colder conditions (and thus a more dependable sea ice regime), would favour larger ringed seal populations, major Pre-Dorset and Dorset prey species. If this correlation is meaningful with respect to the driving factors behind human demographic trends, further study is required to confirm the existence of a similar pattern in other regions of the High Arctic where these human population oscillations have occurred, for example Foxe Basin or Victoria Island.

The decline in ringed seal $\delta^{13}\text{C}$ values during the Thule period relative to the preceding Late Dorset period might signal an increase in open water conditions during this time. These data are therefore consistent with a scenario in which the initial wave of Thule migrants to the Canadian Arctic arrived in a setting that was more conducive to bowhead whale hunting. Furthermore, this transition from colder to warmer conditions characterized by less extensive sea ice may have played a role in the disappearance of the Dorset peoples from the landscape, but the data presented here cannot address this possibility directly. However, it does relate to the question posed above as to why Pre-Dorset and Dorset populations decline during the overall cooling trend if their major prey

species (ringed seals) would have in fact been increasing, or at least more reliable. If instead, warmer conditions (less sea ice) favoured Pre-Dorset and Dorset, then Late Dorset populations should have increased, yet they disappeared. While a Late Dorset disappearance has been suggested by some to be unrelated to the arrival of Thule (Park, 1993), the fact that the disappearance of Late Dorset and the arrival of Thule are essentially contemporaneous suggests this issue has yet to be resolved.

8. Conclusion

Ringed seal bone collagen $\delta^{13}\text{C}$ values from archaeological sites in the Central Canadian Arctic Archipelago varied between 4000 and 500 yr BP. Our interpretation suggests that between 4000 and 800 yr BP the relative contribution of primary productivity derived from sea ice algae increased, consistent with the broad cooling trend observed in the Arctic through the Holocene, before decreasing around 650 yr BP. This decrease in sea ice productivity is associated with the arrival of the Thule population to the Canadian Arctic and supports the notion of more extensive open water conditions at this time.

Overall, the results of this study demonstrate the utility of using marine mammal tissue $\delta^{13}\text{C}$ values to examine the relative importance of sympagic and pelagic production reaching higher trophic

levels in the past. If fluctuations in the amount of sympagic production are greater at lower latitudes, even if the absolute importance of sympagic production is low compared to the CAA, it is possible that the techniques employed here have the potential to address similar issues in regions experiencing more marginal sea ice cover, such as Svalbard, southern Greenland, and the North Water Polynya (Leu et al., 2015), but additional studies are required to confirm this assertion.

CRedit authorship contribution statement

Paul Szpak: Conceptualization, Formal analysis, Funding acquisition, Investigation, Resources, Visualization, Writing - original draft. **James M. Saville:** Conceptualization, Funding acquisition, Investigation, Resources, Writing - review & editing. **James Conolly:** Formal analysis, Investigation, Software, Writing - review & editing. **Michael P. Richards:** Funding acquisition, Resources, Writing - review & editing.

Acknowledgements

Funding was provided by the Social Sciences and Humanities Research Council of Canada, the Natural Sciences and Engineering Research Council of Canada, the Banting Fellowships, and the Canada Foundation for Innovation. We thank the Canadian Museum of History, the Prince of Wales Northern Heritage Centre, and the Government of Nunavut for providing access to the samples. Rebecca Macdonald and Joe Hepburn provided technical assistance.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2019.03.016>.

References

Aagaard, K., Carmack, E.C., 1989. The role of sea ice and other fresh water in the Arctic circulation. *J. Geophys. Res.: Oceans* 94, 14485–14498.

Aagaard, K., Coachman, L.K., Carmack, E., 1981. On the halocline of the Arctic Ocean. *Deep-Sea Res. Part A Oceanogr. Res. Pap.* 28, 529–545.

Altabet, M.A., 2006. Isotopic tracers of the marine nitrogen cycle: present and past. In: Volkman, J.K. (Ed.), *Marine Organic Matter: Biomarkers, Isotopes and DNA*. Springer, Berlin, pp. 251–293.

Altabet, M.A., Francois, R., Murray, D.W., Prell, W.L., 1995. Climate-related variations in denitrification in the Arabian Sea from sediment $^{15}\text{N}/^{14}\text{N}$ ratios. *Nature* 373, 506–509.

Altabet, M.A., Murray, D.W., Prell, W.L., 1999. Climatically linked oscillations in Arabian Sea denitrification over the past 1 m.y.: implications for the marine N cycle. *Paleoceanography* 14, 732–743.

Ambrose, S.H., 1990. Preparation and characterization of bone and tooth collagen for isotopic analysis. *J. Archaeol. Sci.* 17, 431–451.

Arrigo, K.R., Mock, T., Lizotte, M.P., 2010. Primary producers and sea ice. In: Thomas, D.N., Dieckmann, G.S. (Eds.), *Sea Ice*, second ed. Wiley, West Sussex, UK, pp. 283–326.

Barry, R.G., Arundale, W.H., Andrews, J.T., Bradley, R.S., Nichols, H., 1977. Environmental change and cultural change in the eastern Canadian Arctic during the last 5000 years. *Arct. Alp. Res.* 9, 193–210.

Beaumont, W., Beverly, R., Southon, J., Taylor, R.E., 2010. Bone preparation at the KCCAMS laboratory. *Nucl. Instrum. Methods Phys. Res. Sect. B Beam Interact. Mater. Atoms* 268, 906–909.

Becker, B.H., Beissinger, S.R., 2006. Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conserv. Biol.* 20, 470–479.

Belt, S.T., Müller, J., 2013. The Arctic sea ice biomarker IP_{25} : a review of current understanding, recommendations for future research and applications in palaeo sea ice reconstructions. *Quat. Sci. Rev.* 79, 9–25.

Belt, S.T., Vare, L.L., Massé, G., Manners, H.R., Price, J.C., MacLachlan, S.E., Andrews, J.T., Schmidt, S., 2010. Striking similarities in temporal changes to spring sea ice occurrence across the central Canadian Arctic Archipelago over the last 7000 years. *Quat. Sci. Rev.* 29, 3489–3504.

Benoit, D., Simard, Y., Gagné, J., Geoffroy, M., Fortier, L., 2010. From polar night to midnight sun: photoperiod, seal predation, and the diel vertical migrations of polar cod (*Boreogadus saida*) under landfast ice in the Arctic Ocean. *Polar Biol.* 33, 1505–1520.

Bergmann, M.A., Welch, H.E., Butler-Walker, J.E., Siferd, T.D., 1991. Ice algal photosynthesis at Resolute and saqvaquac in the Canadian Arctic. *J. Mar. Syst.* 2, 43–52.

Bevan, A., Colledge, S., Fuller, D., Fyfe, R., Shennan, S., Stevens, C., 2017. Holocene fluctuations in human population demonstrate repeated links to food production and climate. *Proc. Natl. Acad. Sci. Unit. States Am.* 114, E10524.

Bevan, A., Crema, E.R., 2018. Rcarbon v1.2.0: methods for calibrating and analysing radiocarbon dates. <https://CRAN.R-project.org/package=rcarbon>.

Bidigare, R.R., Fluegge, A., Freeman, K.H., Hanson, K.L., Hayes, J.M., Hollander, D., Jasper, J.P., King, L.L., Laws, E.A., Milder, J., Millero, F.J., Pancost, R., Popp, B.N., Steinberg, P.A., Wakeham, S.G., 1997. Consistent fractionation of ^{13}C in nature and in the laboratory: growth-rate effects in some haptophyte algae. *Glob. Biogeochem. Cycles* 11, 279–292.

Birks, H.H., Birks, H.J.B., 2006. Multi-proxy studies in palaeolimnology. *Veg. Hist. Archaeobotany* 15, 235–251.

Birks, H.J.B., Heiri, O., Seppä, H., Bjune, A.E., 2010. Strengths and weaknesses of quantitative climate reconstructions based on late-Quaternary biological proxies. *Open Ecol. J.* 3, 68–110.

Blais, M., Tremblay, J.-E., Jungblut, A.D., Gagnon, J., Martin, J., Thaler, M., Lovejoy, C., 2012. Nitrogen fixation and identification of potential diazotrophs in the Canadian Arctic. *Glob. Biogeochem. Cycles* 26, GB3022.

Bocherens, H., Drucker, D., 2003. Trophic level isotopic enrichment of carbon and nitrogen in bone collagen: case studies from recent and ancient terrestrial ecosystems. *Int. J. Osteoarchaeol.* 13, 46–53.

Boetius, A., Albrecht, S., Bakker, K., Bienhold, C., Felden, J., Fernández-Méndez, M., Hendricks, S., Katlein, C., Lalande, C., Krumpfen, T., Nicolaus, M., Peeken, I., Rabe, B., Rogacheva, A., Rybakova, E., Somavilla, R., Wenzhöfer, F., RV Polarstern ARK27-3-Shipboard Science Party, 2013. Export of algal biomass from the melting Arctic sea ice. *Science* 339, 1430–1432.

Born, E.W., Teilmann, J., Acquarone, M., Riget, F.F., 2004. Habitat use of ringed seals (*Phoca hispida*) in the North Water area (north Baffin Bay). *Arctic* 57, 129–142.

Bradstreet, M.S.W., 1982. Pelagic feeding ecology of dovekeys, *Alle alle*, in Lancaster Sound and western Baffin Bay. *Arctic* 35, 126–140.

Bradstreet, M.S.W., Cross, W.E., 1982. Trophic relationships at high arctic ice edges. *Arctic* 35, 1–12.

Bradstreet, M.S.W., Finley, K.J., Sekerak, A.D., Griffiths, W.B., Evans, C.R., Fabijan, M.F., Stallard, H.E., 1986. Aspects of the Biology of Arctic Cod (*Boreogadus saida*) and its Importance in Arctic Marine Food Chains. Canadian Technical Report of Fisheries and Aquatic Sciences. Department of Fisheries and Oceans, Winnipeg, Manitoba.

Braje, T.J., Rick, T.C., Szpak, P., Newsome, S.D., McCain, J.M., Elliott Smith, E.A., Glassow, M., Hamilton, S.L., 2017. Historical ecology and the conservation of large, hermaphroditic fishes in Pacific Coast kelp forest ecosystems. *Sci. Adv.* 3, e1601759.

Brandes, J.A., Devol, A.H., Yoshinari, T., Jayakumar, D.A., Naqvi, S.W.A., 1998. Isotopic composition of nitrate in the central Arabian Sea and eastern tropical North Pacific: a tracer for mixing and nitrogen cycles. *Limnol. Oceanogr.* 43, 1680–1689.

Briner, J.P., McKay, N.P., Axford, Y., Bennike, O., Bradley, R.S., de Vernal, A., Fisher, D., Francus, P., Fréchette, B., Gajewski, K., Jennings, A., Kaufman, D.S., Miller, G., Rouston, C., Wagner, B., 2016. Holocene climate change in Arctic Canada and Greenland. *Quat. Sci. Rev.* 147, 340–364.

Briner, J.P., Michelutti, N., Francis, D.R., Miller, G.H., Axford, Y., Wooller, M.J., Wolfe, A.P., 2006. A multi-proxy lacustrine record of Holocene climate change on northeastern Baffin Island, Arctic Canada. *Quat. Res.* 65, 431–442.

Brown, T.A., Nelson, D.E., Vogel, J.S., Southon, J.R., 1988. Improved collagen extraction by modified Longin method. *Radiocarbon* 30, 171–177.

Bump, J.K., Fox-Dobbs, K., Bada, J.L., Koch, P.L., Peterson, R.O., Vucetich, J.A., 2007. Stable isotopes, ecological integration and environmental change: wolves record atmospheric carbon isotope trend better than tree rings. *Proc. Biol. Sci.* 274, 2471–2480.

Burkhardt, S., Riebesell, U., Zondervan, I., 1999a. Effects of growth rate, CO_2 concentration, and cell size on the stable carbon isotope fractionation in marine phytoplankton. *Geochem. Cosmochim. Acta* 63, 3729–3741.

Burkhardt, S., Riebesell, U., Zondervan, I., 1999b. Stable carbon isotope fractionation by marine phytoplankton in response to daylength, growth rate, and CO_2 availability. *Mar. Ecol. Prog. Ser.* 184, 31–41.

Burton, R.K., Snodgrass, J.J., Gifford-Gonzalez, D., Guilderson, T., Brown, T., Koch, P.L., 2001. Holocene changes in the ecology of northern fur seals: insights from stable isotopes and archaeofauna. *Oecologia* 128, 107–115.

Capone, D.G., Zehr, J.P., Paerl, H.W., Bergman, B., Carpenter, E.J., 1997. *Trichodesmium*, a globally significant marine cyanobacterium. *Science* 276, 1221.

Carpenter, E.J., Capone, D.G., 2008. Nitrogen fixation in the marine environment. In: Capone, D.G., Bronk, D.A., Mulholland, M.R., Carpenter, E.J. (Eds.), *Nitrogen in the Marine Environment*, second ed. Elsevier, Amsterdam, pp. 141–198.

Carpenter, E.J., Harvey, H.R., Fry, B., Capone, D.G., 1997. Biogeochemical tracers of the marine cyanobacterium *Trichodesmium*. *Deep Sea Res. Oceanogr. Res. Pap.* 44, 27–38.

Casciotti, K.L., 2016. Nitrogen and oxygen isotopic studies of the marine nitrogen cycle. *Ann. Rev. Mar. Sci.* 8, 379–407.

Chaput, M.A., Gajewski, K., 2016. Radiocarbon dates as estimates of ancient human population size. *Anthropocene* 15, 3–12.

Cherel, Y., Hobson, K.A., 2007. Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar. Ecol. Prog. Ser.* 329, 281–287.

- Cline, J.D., Kaplan, I.R., 1975. Isotopic fractionation of dissolved nitrate during denitrification in the eastern tropical North Pacific Ocean. *Mar. Chem.* 3, 271–299.
- Comiso, J.C., 2010. Variability and trends of global sea ice cover. In: Thomas, D.N., Dieckmann, G.S. (Eds.), *Sea Ice*, second ed. Wiley, West Sussex, UK, pp. 205–246.
- Cornelisen, C.D., Wing, S.R., Clark, K.L., Bowman, M.H., Frew, R.D., Hurd, C.L., 2007. Patterns in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signature of *Ulva pertusa*: interaction between physical gradients and nutrient source pools. *Limnol. Oceanogr.* 52, 820–832.
- Cota, G.F., Legendre, L., Gosselin, M., Ingram, R.G., 1991. Ecology of bottom ice algae: I. Environmental controls and variability. *J. Mar. Syst.* 2, 257–277.
- Crawford, R.E., Jorgenson, J.K., 1996. Quantitative studies of arctic cod (*Boreogadus saida*) schools: important energy stores in the arctic food web. *Arctic* 49, 181–193.
- Crema, E.R., Habu, J., Kobayashi, K., Madella, M., 2016. Summed probability distribution of ^{14}C dates suggests regional divergences in the population dynamics of the Jomon Period in eastern Japan. *PLoS One* 11, e0154809.
- Cronin, T.M., Dwyer, G.S., Kamiya, T., Schwede, S., Willard, D.A., 2003. Medieval warm period, little ice age and 20th century temperature variability from Chesapeake Bay. *Glob. Planet. Chang.* 36, 17–29.
- Cronin, T.M., Gemery, L., Briggs Jr., W.M., Jakobsson, M., Polyak, L., Brouwers, E.M., 2010. Quaternary Sea-ice history in the Arctic Ocean based on a new Ostracode sea-ice proxy. *Quat. Sci. Rev.* 29, 3415–3429.
- Cullen, J.T., Rosenthal, Y., Falkowski, P.G., 2001. The effect of anthropogenic CO_2 on the carbon isotope composition of marine phytoplankton. *Limnol. Oceanogr.* 46, 996–998.
- Curran, A., Jacobi, R., 2001. A formal mammalian biostratigraphy for the Late Pleistocene of Britain. *Quat. Sci. Rev.* 20, 1707–1716.
- Curry, J.A., Schramm, J.L., Ebert, E.E., 1995. Sea ice-albedo climate feedback mechanism. *J. Clim.* 8, 240–247.
- Darnis, G., Robert, D., Pomerleau, C., Link, H., Archambault, P., Nelson, R.J., Geoffroy, M., Tremblay, J.-É., Lovejoy, C., Ferguson, S., Hunt, B.V., Fortier, L., 2012. Current state and trends in Canadian Arctic marine ecosystems: II. Heterotrophic food web, pelagic-benthic coupling, and biodiversity. *Clim. Change* 115, 179–205.
- Darwent, C.M., 2001. High Arctic Paleoeskimo Fauna: Temporal Changes and Regional Differences. University of Missouri, Columbia, Missouri, p. 203.
- de Vernal, A., Hillaire-Marcel, C., Darby, D.A., 2005. Variability of sea ice cover in the Chukchi Sea (western Arctic Ocean) during the Holocene. *Paleoceanography* 20, PA4018.
- Dekin, A.A., 1972. Climatic change and cultural change: a correlative study from eastern Arctic prehistory. *Polar Notes* 12, 11–31.
- DeNiro, M.J., 1985. Postmortem preservation and alteration of *in vivo* bone collagen isotope ratios in relation to palaeodietary reconstruction. *Nature* 317, 806–809.
- Dieckmann, G.S., Hellmer, H.H., 2010. The importance of sea ice: an overview. In: Thomas, D.N., Dieckmann, G.S. (Eds.), *Sea Ice*, second ed. Wiley, West Sussex, UK, pp. 1–22.
- Dorado, S., Roeker, J.R., Wissel, B., Quigg, A., 2012. Isotope baseline shifts in pelagic food webs of the Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 464, 37–49.
- Duggins, D.O., Gómez-Buckley, M.C., Buckley, R.M., Lowe, A.T., Galloway, A.W.E., Dethier, M.N., 2016. Islands in the stream: kelp detritus as faunal magnets. *Mar. Biol.* 163, 1–17.
- Duggins, D.O., Simenstad, C.A., Estes, J.A., 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245, 170–173.
- Dunton, K.H., Saupé, S.M., Golikov, A.N., Schell, D.M., Schonberg, S.V., 1989. Trophic relationships and isotopic gradients among arctic and subarctic marine fauna. *Mar. Ecol. Prog. Ser.* 56, 89–97.
- Durbin, E.G., Casas, M.C., 2014. Early reproduction by *Calanus glacialis* in the Northern Bering Sea: the role of ice algae as revealed by molecular analysis. *J. Plankton Res.* 36, 523–541.
- Dyke, A.S., Hooper, J., Harington, C.R., Savelle, J.M., 1999. The Late Wisconsinan and Holocene record of walrus (*Odobenus rosmarus*) from North America: a review with new data from Arctic and Atlantic Canada. *Arctic* 52, 160–181.
- Dyke, A.S., Hooper, J., Savelle, J.M., 1996. A history of sea ice in the Canadian Arctic Archipelago based on postglacial remains of the bowhead whale (*Balaena mysticetus*). *Arctic* 49, 235–255.
- Dyke, A.S., Savelle, J.M., 2009. Paleoeskimo demography and sea-level history, Kent Peninsula and King William Island, Central Northwest Passage, Arctic Canada. *Arctic* 62, 371–392.
- Dyke, A.S., Savelle, J.M., Johnson, D.S., 2011. Paleoeskimo demography and Holocene sea-level history, Gulf of Boothia, Arctic Canada. *Arctic* 64, 155–168.
- Dyke, A.S., Savelle, J.M., Szpak, P., Southon, J.R., Howse, L., Desrosiers, P.M., Kotar, K., 2019. An assessment of marine reservoir corrections for radiocarbon dates on walrus from the Foxe Basin region of Arctic Canada. *Radiocarbon* 61, 67–81.
- Ebert, E.E., Curry, J.A., 1993. An intermediate one-dimensional thermodynamic sea ice model for investigating ice-atmosphere interactions. *J. Geophys. Res.: Oceans* 98, 10085–10109.
- Emslie, S.D., Patterson, W.P., 2007. Abrupt recent shift in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in Adélie penguin eggshell in Antarctica. *Proc. Natl. Acad. Sci. Unit. States Am.* 104, 11666–11669.
- English, P.A., Green, D.J., Nocera, J.J., 2018. Stable isotopes from museum specimens may provide evidence of long-term change in the trophic ecology of a migratory aerial insectivore. *Front. Ecol. Evol.* 6.
- Ershova, E.A., Hopcroft, R.R., Kosobokova, K.N., Matsuno, K., Nelson, R.J., Yamaguchi, A., Eisner, L.B., 2015. Long-term changes in summer zooplankton communities of the western Chukchi Sea, 1945–2012. *Oceanography* 28, 100–115.
- Falk-Petersen, S., Mayzaud, P., Kattner, G., Sargent, J.R., 2009. Lipids and life strategy of Arctic *Calanus*. *Mar. Biol. Res.* 5, 18–39.
- Falk-Petersen, S., Pavlov, V., Timofeev, S., Sargent, J., 2007. Climate variability and possible effects on arctic food chains: the role of *Calanus*. In: Ørbæk, J.B., Kallenborn, R., Tombre, I., Hegseth, E.N., Falk-Petersen, S., Hoel, A.H. (Eds.), *Arctic Alpine Ecosystems and People in a Changing Environment*. Springer, Berlin, pp. 147–166.
- Ferguson, S.H., Stirling, I., McLoughlin, P., 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. *Mar. Mamm. Sci.* 21, 121–135.
- Finkelstein, S.A., Ross, J.M., Adams, J.K., 2009. Spatiotemporal variability in arctic climates of the past millennium: implications for the study of Thule culture on Melville Peninsula, Nunavut. *Arctic Antarct. Alpine Res.* 41, 442–454.
- Fisher, D.A., Koerner, R.M., Bourgeois, J.C., Zielinski, G., Wake, C., Hammer, C.U., Clausen, H.B., Gundestrup, N., Johnsen, S., Goto-Azuma, K., Hondoh, T., Blake, E., Gerasimoff, M., 1998. Penny ice Cap cores, Baffin Island, Canada, and the Wisconsinan Foxe Dome connection: two states of Hudson Bay ice cover. *Science* 279, 692–695.
- Fisher, D.A., Koerner, R.M., Paterson, W.S.B., Dansgaard, W., Gundestrup, N., Reeh, N., 1983. Effect of wind scouring on climatic records from ice-core oxygen-isotope profiles. *Nature* 301, 205–209.
- Fisher, D.A., Koerner, R.M., Reeh, N., 1995. Holocene climatic records from Agassiz Ice Cap, Ellesmere Island, NWT, Canada. *Holocene* 5, 19–24.
- Fontoura, N.F., Rodrigues, L.R., Batista, C.B., Persch, T.S.P., Janowicz, M.E., 2015. Integrating ontogenetic shift, growth and mortality to determine a species' ecological role from isotopic signatures. *PLoS One* 10, e0125059.
- Forest, A., Galindo, V., Darnis, G., Pineault, S., Lalande, C., Tremblay, J.-É., Fortier, L., 2011a. Carbon biomass, elemental ratios (C:N) and stable isotopic composition ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of dominant calanoid copepods during the winter-to-summer transition in the Amundsen Gulf (Arctic Ocean). *J. Plankton Res.* 33, 161–178.
- Forest, A., Tremblay, J.-É., Gratton, Y., Martin, J., Gagnon, J., Darnis, G., Sampei, M., Fortier, L., Ardyna, M., Gosselin, M., Hattori, H., Nguyen, D., Maranger, R., Vagué, D., Marrasé, C., Pedrós-Alió, C., Sallon, A., Michel, C., Kellogg, C., Deming, J., Shadwick, E., Thomas, H., Link, H., Archambault, P., Piepenburg, D., 2011b. Biogenic carbon flows through the planktonic food web of the Amundsen Gulf (Arctic Ocean): a synthesis of field measurements and inverse modeling analyses. *Prog. Oceanogr.* 91, 410–436.
- Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R.B., Aschan, M.M., Dolgov, A.V., 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nat. Clim. Change* 5, 673.
- France, R., Loret, J., Mathews, R., Springer, J., 1998. Longitudinal variation in zooplankton $\delta^{13}\text{C}$ through the Northwest Passage: inference for incorporation of sea-ice POM into pelagic foodwebs. *Polar Biol.* 20, 335–341.
- France, R.L., 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Mar. Ecol. Prog. Ser.* 124, 307–312.
- Francis, D.R., Wolfe, A.P., Walker, I.R., Miller, G.H., 2006. Inter-glacial and Holocene temperature reconstructions based on midge remains in sediments of two lakes from Baffin Island, Nunavut, Arctic Canada. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 236, 107–124.
- Friesen, T.M., Arnold, C.D., 2008. The timing of the Thule migration: new dates from the western Canadian Arctic. *Am. Antiq.* 73, 527–538.
- Furze, M.F.A., Piñkowski, A.J., Coulthard, R.D., 2014. New cetacean ΔR values for Arctic North America and their implications for marine-mammal-based palaeoenvironmental reconstructions. *Quat. Sci. Rev.* 91, 218–241.
- Gajewski, K., 2015. Quantitative reconstruction of Holocene temperatures across the Canadian Arctic and Greenland. *Glob. Planet. Chang.* 128, 14–23.
- Giordani, P., Helder, W., Koning, E., Misericocchi, S., Danovaro, R., Malaguti, A., 2002. Gradients of benthic–pelagic coupling and carbon budgets in the Adriatic and Northern Ionian Sea. *J. Mar. Syst.* 33, 365–387.
- Gorlova, E., Krylovich, O., Savinetsky, A., Khasanov, B., 2012. Ecology of the ringed seal (*Pusa hispida*) from the Bering Strait in the late Holocene. *Biol. Bull.* 39, 464–471.
- Gorlova, E.N., Krylovich, O.A., Tiunov, A.V., Khasanov, B.F., Vasyukov, D.D., Savinetsky, A.B., 2015. Stable-isotope analysis as a method of taxonomical identification of archaeozoological material. *Archaeol. Ethnol. Anthropol. Eurasia* 43, 110–121.
- Gosselin, M., Levasseur, M., Wheeler, P.A., Horner, R.A., Booth, B.C., 1997. New measurements of phytoplankton and ice algal production in the Arctic Ocean. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 44, 1623–1644.
- Gradinger, R., 2009. Sea-ice algae: major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 56, 1201–1212.
- Graham, B.S., Grubbs, D., Holland, K., Popp, B.N., 2007. A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. *Mar. Biol.* 150, 647–658.
- Grayson, D.K., 1989. The chronology of North American Late Pleistocene extinctions. *J. Archaeol. Sci.* 16, 153–165.
- Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A., McNutt, S.L., 2006. A major ecosystem shift in the northern Bering Sea. *Science* 311, 1461–1464.
- Guiry, E.J., Szpak, P., Richards, M.P., 2016. Effects of lipid extraction and ultrafiltration on stable carbon and nitrogen isotopic compositions of fish bone collagen. *Rapid Commun. Mass Spectrom.* 30, 1591–1600.
- Hamilton, C.D., Kovacs, K.M., Ims, R.A., Aars, J., Lydersen, C., 2017. An Arctic

- predator–prey system in flux: climate change impacts on coastal space use by polar bears and ringed seals. *J. Anim. Ecol.* 86, 1054–1064.
- Hamilton, C.D., Lydersen, C., Ims, R.A., Kovacs, K.M., 2015. Predictions replaced by facts: a keystone species' behavioural responses to declining arctic sea-ice. *Biol. Lett.* 11.
- Hamilton, S.L., Caselle, J.E., Lantz, C.A., Egloff, T.L., Kondo, E., Newsome, S.D., Loke-Smith, K., Pondella, D.J., II, Young, K.A., Lowe, C.G., 2011. Extensive geographic and ontogenetic variation characterizes the trophic ecology of a temperate reef fish on southern California (USA) rocky reefs. *Mar. Ecol. Prog. Ser.* 429, 227–244.
- Hannah, C.G., Dupont, F., Dunphy, M., 2009. Polynyas and tidal currents in the Canadian Arctic Archipelago. *Arctic* 62, 83–95.
- Harada, N., 2016. Potential catastrophic reduction of sea ice in the western Arctic Ocean: its impact on biogeochemical cycles and marine ecosystems. *Glob. Planet. Chang.* 136, 1–17.
- Harington, C.R., 2011. Pleistocene vertebrates of the Yukon Territory. *Quat. Sci. Rev.* 30, 2341–2354.
- Hedges, R.E.M., Clement, J.G., Thomas, D.L., O'Connell, T.C., 2007. Collagen turnover in the adult femoral mid-shaft: modeled from anthropogenic radiocarbon tracer measurements. *Am. J. Phys. Anthropol.* 133, 808–816.
- Hinzman, L.D., Deal, C.J., McGuire, A.D., Mernild, S.H., Polyakov, I.V., Walsh, J.E., 2013. Trajectory of the Arctic as an integrated system. *Ecol. Appl.* 23, 1837–1868.
- Hobson, K.A., 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. *Mar. Ecol. Prog. Ser.* 95, 7–18.
- Hobson, K.A., Ambrose Jr., W.G., Renaud, P.E., 1995. Sources of primary production, benthic–pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar. Ecol. Prog. Ser.* 128, 1–10.
- Hobson, K.A., Fisk, A., Karnovsky, N., Holst, M., Gagnon, J.-M., Fortier, M., 2002. A stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 49, 5131–5150.
- Hobson, K.A., Piatt, J.F., Pitocchelli, J., 1994. Using stable isotopes to determine seabird trophic relationships. *J. Anim. Ecol.* 63, 786–798.
- Hobson, K.A., Welch, H.E., 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar. Ecol. Prog. Ser.* 84, 9–18.
- Hodgetts, L., Wells, P., 2016. Priscilla Renouf remembered: an introduction to the special issue with a note on renaming the Palaeoeskimo Tradition. *Arctic* 69 i–vi.
- Holland, M.M., Bitz, C.M., 2003. Polar amplification of climate change in coupled models. *Clim. Dyn.* 21, 221–232.
- Holst, M., Stirling, I., Hobson, K.A., 2001. Diet of ringed seals (*Phoca hispida*) on the east and west sides of the North Water Polynya, northern Baffin Bay. *Mar. Mamm. Sci.* 17, 888–908.
- Hop, H., Gjøsæter, H., 2013. Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. *Mar. Biol. Res.* 9, 878–894.
- Hop, H., Welch, H.E., Crawford, R.E., 1997. Population Structure and Feeding Ecology of Arctic Cod Schools in the Canadian High Arctic, vol. 19. American Fisheries Society Symposium.
- Horner, R., Schrader, G.C., 1982. Relative contributions of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. *Arctic* 35, 485–503.
- Laidre, K.L., Stirling, I., Lowry, L.F., Wiig, Ø., Heide-Jørgensen, M.P., Ferguson, S.H., 2008. Quantifying the sensitivity of arctic marine mammals to climate-induced habitat change. *Ecol. Appl.* 18, S97–S125.
- Iorio, C.J., 2005. A Detailed Analysis of Ringed Seal Remains (*Phoca hispida*) from Three Seasonally Different Thule Sites at Hazard Inlet, Somerset Island (Nunavut), Anthropology. McGill University, Montreal, Canada, p. 219.
- Ji, R., Jin, M., Varpe, Ø., 2013. Sea ice phenology and timing of primary production pulses in the Arctic Ocean. *Glob. Chang. Biol.* 19, 734–741.
- Jones, E.P., Swift, J.H., Anderson, L.G., Lipizer, M., Civitarese, G., Falkner, K.K., Kattner, G., McLaughlin, F., 2003. Tracing Pacific water in the North Atlantic Ocean. *J. Geophys. Res.* 108, 3116.
- Karnovsky, N., Ainley, D.G., Lee, P., 2007. The impact and importance of production in polynyas to top-trophic predators: three case histories. In: Smith, W.O., Barber, D.G. (Eds.), *Polynyas: Windows to the World*. Elsevier Science, Amsterdam, pp. 391–410.
- Karnovsky, N.J., Hobson, K.A., Iverson, S., Hunt Jr., G.L., 2008. Seasonal changes in diets of seabirds in the North Water Polynya: a multiple-indicator approach. *Mar. Ecol. Prog. Ser.* 357, 291–299.
- Kaufman, D.S., Ager, T.A., Anderson, N.J., Anderson, P.M., Andrews, J.T., Bartlein, P.J., Brubaker, L.B., Coats, L.L., Cwynar, L.C., Duvall, M.L., Dyke, A.S., Edwards, M.E., Eisner, W.R., Gajewski, K., Geirsdóttir, A., Hu, F.S., Jennings, A.E., Kaplan, M.R., Kerwin, M.W., Lozhkin, A.V., MacDonald, G.M., Miller, G.H., Mock, C.J., Oswald, W.W., Otto-Bliesner, B.L., Porinchu, D.F., Rühland, K., Smol, J.P., Steig, E.J., Wolfe, B.B., 2004. Holocene thermal maximum in the western Arctic (0–180°W). *Quat. Sci. Rev.* 23, 529–560.
- Kędra, M., Moritz, C., Choy, E.S., David, C., Degen, R., Duerksen, S., Ellingsen, I., Górska, B., Grebmeier, J.M., Kirievskaya, D., van Oevelen, D., Piwosz, K., Samuelsen, A., Węślawski, J.M., 2015. Status and trends in the structure of Arctic benthic food webs. *Polar Res.* 34, 23776.
- Kirchmeier-Young, M.C., Zwieters, F.W., Gillett, N.P., 2016. Attribution of extreme events in Arctic sea ice extent. *J. Clim.* 30, 553–571.
- Koch, P.L., Fox-Dobbs, K., Newsome, S.D., 2009. The isotopic ecology of fossil vertebrates and conservation paleobiology. In: Dietl, G.P., Flessa, K.W. (Eds.), *Conservation Paleobiology: Using the Past to Manage for the Future*, Paleontological Society Short Course, October 17th, 2009. The Paleontological Society Papers, vol. 15. The Paleontological Society, Lubbock, TX, pp. 95–112.
- Kohlbach, D., Graeve, M., Lange, A., David, C., Peeken, I., Flores, H., 2016. The importance of ice algae-produced carbon in the central Arctic Ocean ecosystem: food web relationships revealed by lipid and stable isotope analyses. *Limnol. Oceanogr.* 61, 2027–2044.
- Kohlbach, D., Schaafsma, F.L., Graeve, M., Lebreton, B., Lange, B.A., David, C., Vortkamp, M., Flores, H., 2017. Strong linkage of polar cod (*Boreogadus saida*) to sea ice algae-produced carbon: evidence from stomach content, fatty acid and stable isotope analyses. *Prog. Oceanogr.* 152, 62–74.
- Kopczyńska, E.E., Goeyens, L., Semeneh, M., Dehairs, F., 1995. Phytoplankton composition and cell carbon distribution in Prydz Bay, Antarctica: relation to organic particulate matter and its $\delta^{13}\text{C}$ values. *J. Plankton Res.* 17, 685–707.
- Kopp, D., Lefebvre, S., Cachera, M., Villanueva, M.C., Ernande, B., 2015. Reorganization of a marine trophic network along an inshore–offshore gradient due to stronger pelagic–benthic coupling in coastal areas. *Prog. Oceanogr.* 130, 157–171.
- Korb, R.E., Raven, J.A., Johnston, A.M., Leftley, J.W., 1996. Effects of cell size and specific growth rate on stable carbon isotope discrimination by two species of marine diatom. *Mar. Ecol. Prog. Ser.* 143, 283–288.
- Kroopnick, P.M., 1985. The distribution of ^{13}C of ΣCO_2 in the world oceans. *Deep-Sea Res. Part A Oceanogr. Res. Pap.* 32, 57–84.
- Krylovich, O.A., 2011. Hunting impacts on the sea otter (*Enhydra lutris*) population in Clam Lagoon (Adak Island, Aleutian Islands) 7,000 Years ago? Results of preliminary stable isotopes analysis. *J. Isl. Coast. Archaeol.* 6, 155–159.
- Laidre, K.L., Heide-Jørgensen, M.P., Gissel Nielsen, T., 2007. Role of the bowhead whale as a predator in West Greenland. *Mar. Ecol. Prog. Ser.* 346, 285–297.
- Lavoie, D., Denman, K., Michel, C., 2005. Modeling ice algal growth and decline in a seasonally ice-covered region of the Arctic (Resolute Passage, Canadian Archipelago). *J. Geophys. Res.* 110, C11009.
- Laws, E.A., Popp, B.N., Bidigare, R.R., Kennicutt, M.C., Macko, S.A., 1995. Dependence of phytoplankton carbon isotopic composition on growth rate and $[\text{CO}_2]_{\text{aq}}$: theoretical considerations and experimental results. *Geochim. Cosmochim. Acta* 59, 1131–1138.
- Ledu, D., Rochon, A., de Vernal, A., Barletta, F., St-Onge, G., 2010. Holocene sea ice history and climate variability along the main axis of the Northwest Passage, Canadian Arctic. *Paleoceanography* 25, PA2213.
- LeMoine, G., Helmer, J., Grønnow, B., 2003. Late Dorset architecture on Little Cornwallis Island, Nunavut. *Inuit Stud.* 27, 255–280.
- Leu, E., Mundy, C.J., Assmy, P., Campbell, K., Gabrielsen, T.M., Gosselin, M., Juul-Pedersen, T., Gradinger, R., 2015. Arctic spring awakening – steering principles behind the phenology of vernal ice algal blooms. *Prog. Oceanogr.* 139, 151–170.
- Leu, E., Søreide, J.E., Hessen, D.O., Falk-Petersen, S., Berge, J., 2011. Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. *Prog. Oceanogr.* 90, 18–32.
- Luque, S.P., Ferguson, S.H., Breed, G.A., 2014. Spatial behaviour of a keystone Arctic marine predator and implications of climate warming in Hudson Bay. *J. Exp. Mar. Biol. Ecol.* 461, 504–515.
- Maberly, S., Raven, J., Johnston, A., 1992. Discrimination between ^{12}C and ^{13}C by marine plants. *Oecologia* 91, 481–492.
- Macias Fauria, M., Grinsted, A., Helama, S., Moore, J., Timonen, M., Martma, T., Isaksson, E., Eronen, M., 2010. Unprecedented low twentieth century winter sea ice extent in the Western Nordic Seas since A.D. 1200. *Clim. Dyn.* 34, 781–795.
- Mann, M.E., Zhang, Z., Hughes, M.K., Bradley, R.S., Miller, S.K., Rutherford, S., Ni, F., 2008. Proxy-based reconstructions of hemispheric and global surface temperature variations over the past two millennia. *Proc. Natl. Acad. Sci. Unit. States Am.* 105, 13252–13257.
- Massé, G., Rowland, S.J., Sicre, M.-A., Jacob, J., Jansen, E., Belt, S.T., 2008. Abrupt climate changes for Iceland during the last millennium: evidence from high resolution sea ice reconstructions. *Earth Planet. Sci. Lett.* 269, 565–569.
- Matley, J.K., Fisk, A.T., Dick, T.A., 2013. The foraging ecology of arctic cod (*Boreogadus saida*) during open water (July–August) in Allen Bay, arctic Canada. *Mar. Biol.* 160, 2993–3004.
- Matley, J.K., Fisk, A.T., Dick, T.A., 2015. Foraging ecology of ringed seals (*Pusa hispida*), beluga whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in the Canadian High Arctic determined by stomach content and stable isotope analysis. *Polar Res.* 34, 24295.
- Maykut, G.A., Untersteiner, N., 1971. Some results from a time-dependent thermodynamic model of sea ice. *J. Geophys. Res.* 76, 1550–1575.
- McCartney, A.P., 1977. Thule Eskimo Prehistory along Northwestern Hudson Bay. Archaeological Survey of Canada Paper No. 70. National Museums of Canada, Ottawa.
- McCartney, A.P., 1979. A processual consideration of Thule whale bone houses. In: McCartney, A.P. (Ed.), *Thule Eskimo Culture: an Anthropological Retrospective*. Archaeological Survey of Canada Paper No. 88. National Museums of Canada, Ottawa, pp. 301–323.
- McClelland, J.W., Holl, C.M., Montoya, J.P., 2003. Relating low $\delta^{15}\text{N}$ values of zooplankton to N_2 -fixation in the tropical North Atlantic: insights provided by stable isotope ratios of amino acids. *Deep Sea Res. Oceanogr. Res. Pap.* 50, 849–861.
- McConnaughey, T., McRoy, C.P., 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. *Mar. Biol.* 53, 257–262.
- McGhee, R., 1969/1970. Speculations on climatic change and Thule culture development. *Folk* 11/12, 173–184.

- McGhee, R., 1979. The Palaeoeskimo Occupations at Port Refuge, High Arctic Canada. National Museums of Canada, Ottawa.
- McGovern, T.H., 1991. Climate, correlation, and causation in Norse Greenland. *Arctic Anthropol.* 28, 77–100.
- McLaren, I.A., 1958. The Biology of the Ringed Seal (*Phoca hispida* Schreber) in the Eastern Canadian Arctic. Bulletin of the Fisheries Research Board of Canada. Fisheries Research Board of Canada, Ottawa.
- McMahon, K.W., Ambrose Jr., W.G., Johnson, B.J., Sun, M.-Y., Lopez, G.R., Clough, L.M., Carroll, M.L., 2006. Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. *Mar. Ecol. Prog. Ser.* 310, 1–14.
- McMeans, B.C., Rooney, N., Arts, M.T., Fisk, A.T., 2013. Food web structure of a coastal Arctic marine ecosystem and implications for stability. *Mar. Ecol. Prog. Ser.* 482, 17–28.
- McMullin, R.M., Wing, S.R., Wing, L.C., Shatova, O.A., 2017. Trophic position of Antarctic ice fishes reflects food web structure along a gradient in sea ice persistence. *Mar. Ecol. Prog. Ser.* 564, 87–98.
- Meckler, A.N., Ren, H., Sigman, D.M., Gruber, N., Plessen, B., Schubert, C.J., Haug, G.H., 2011. Deglacial nitrogen isotope changes in the Gulf of Mexico: evidence from bulk sedimentary and foraminifera-bound nitrogen in Orca Basin sediments. *Paleoceanography* 26, PA4216.
- Michel, C., Ingram, R.G., Harris, L.R., 2006. Variability in oceanographic and ecological processes in the Canadian Arctic Archipelago. *Prog. Oceanogr.* 71, 379–401.
- Michel, C., Legendre, L., Ingram, R.G., Gosselin, M., Levasseur, M., 1996. Carbon budget of sea-ice algae in spring: evidence of a significant transfer to zooplankton grazers. *J. Geophys. Res. Oceans* 101, 18345–18360.
- Miller, G.H., Alley, R.B., Brigham-Grette, J., Fitzpatrick, J.J., Polyak, L., Serreze, M.C., White, J.W.C., 2010a. Arctic amplification: can the past constrain the future? *Quat. Sci. Rev.* 29, 1779–1790.
- Miller, G.H., Brigham-Grette, J., Alley, R.B., Anderson, L., Bauch, H.A., Douglas, M.S.V., Edwards, M.E., Elias, S.A., Finney, B.P., Fitzpatrick, J.J., Funder, S.V., Herbert, T.D., Hinzman, L.D., Kaufman, D.S., MacDonald, G.M., Polyak, L., Robock, A., Serreze, M.C., Smol, J.P., Spielhagen, R., White, J.W.C., Wolfe, A.P., Wolff, E.W., 2010b. Temperature and precipitation history of the Arctic. *Quat. Sci. Rev.* 29, 1679–1715.
- Milne, S.B., Park, R.W., 2016. Pre-Dorset culture. In: Friesen, T.M., Mason, O.K. (Eds.), *The Oxford Handbook of the Prehistoric Arctic*. Oxford University Press, Oxford, pp. 693–712.
- Minagawa, M., Wada, E., 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim. Cosmochim. Acta* 48, 1135–1140.
- Misarti, N., Finney, B.P., Maschner, H., Wooller, M.J., 2009. Changes in northeast Pacific marine ecosystems over the last 4500 years: evidence from stable isotope analysis of bone collagen from archaeological middens. *Holocene* 19, 1139–1151.
- Montoya, J.P., 2008. Nitrogen stable isotopes in marine environments. In: Capone, D.G., Bronk, D.A., Mulholland, M.R., Carpenter, E.J. (Eds.), *Nitrogen in the Marine Environment*, second ed. Elsevier, Amsterdam, pp. 1277–1302.
- Moody, J.F., Hodgetts, L.M., 2013. Subsistence practices of pioneering Thule–Inuit: a faunal analysis of Tiktaalik. *Arctic Anthropol.* 50, 4–24.
- Mook, W.G., Bommerson, J.C., Staverman, W.H., 1974. Carbon isotope fractionation between dissolved bicarbonate and gaseous carbon dioxide. *Earth Planet. Sci. Lett.* 22, 169–176.
- Moore, J.J., Hugen, K.A., Miller, G.H., Overpeck, J.T., 2001. Little Ice Age recorded in summer temperature reconstruction from varved sediments of Donard Lake, Baffin Island, Canada. *J. Paleolimnol.* 25, 503–517.
- Moore, S.E., Huntington, H.P., 2008. Arctic marine mammals and climate change: impacts and resilience. *Ecol. Appl.* 18, S157–S165.
- Moore, S.E., Reeves, R.R., 2018. Tracking arctic marine mammal resilience in an era of rapid ecosystem alteration. *PLoS Biol.* 16, e2006708.
- Moss, M.L., Yang, D.Y., Newsome, S.D., Speller, C.F., McKechnie, I., McMillan, A.D., Losey, R.J., Koch, P.L., 2006. Historical ecology and biogeography of North Pacific pinnipeds: isotopes and ancient DNA from three archaeological assemblages. *J. Isl. Coast. Archaeol.* 1, 165–190.
- Mueller, B.L., Gillett, N.P., Monahan, A.H., Zwiers, F.W., 2018. Attribution of Arctic sea ice decline from 1953 to 2012 to influences from natural, greenhouse gas, and anthropogenic aerosol forcing. *J. Clim.* 31, 7771–7787.
- Mundy, C.J., Barber, D.G., Michel, C., 2005. Variability of snow and ice thermal, physical and optical properties pertinent to sea ice algae biomass during spring. *J. Mar. Syst.* 58, 107–120.
- Murray, M.S., 1999. Local heroes. The long-term effects of short-term prosperity - an example from the Canadian Arctic. *World Archaeol.* 30, 466–483.
- Murray, M.S., 2005. Prehistoric use of ringed seals: a zooarchaeological study from Arctic Canada. *Environ. Archaeol.* 10, 19–38.
- Najafi, M.R., Zwiers, F.W., Gillett, N.P., 2015. Attribution of Arctic temperature change to greenhouse-gas and aerosol influences. *Nat. Clim. Change* 5, 246.
- Newsome, S.D., Etnier, M.A., Kurl, C.M., Waldbauer, J.R., Chamberlain, C.P., Koch, P.L., 2007. Historic decline in primary productivity in western Gulf of Alaska and eastern Bering Sea: isotopic analysis of northern fur seal teeth. *Mar. Ecol. Prog. Ser.* 332, 211–224.
- North Greenland Ice Core Project Members, 2004. High-resolution record of Northern Hemisphere climate extending into the last interglacial period. *Nature* 431, 147–151.
- Nøst Hegseth, E., 1998. Primary production of the Northern Barents Sea. *Polar Res.* 17, 113–123.
- Nozais, C., Gosselin, M., Michel, C., Tita, G., 2001. Abundance, biomass, composition and grazing impact of the sea-ice meiofauna in the North Water, northern Baffin Bay. *Mar. Ecol. Prog. Ser.* 217, 235–250.
- Osmond, C.B., Valaane, N., Haslam, S.M., Uotila, P., Roksandic, Z., 1981. Comparisons of $\delta^{13}\text{C}$ values in leaves of aquatic macrophytes from different habitats in Britain and Finland; some implications for photosynthetic processes in aquatic plants. *Oecologia* 50, 117–124.
- Ostrom, P.H., Wiley, A.E., James, H.F., Rossman, S., Walker, W.A., Zipkin, E.F., Chikaraishi, Y., 2017. Broad-scale trophic shift in the pelagic North Pacific revealed by an oceanic seabird. *Proc. Biol. Sci.* 284, 1851.
- Park, R.W., 1993. The Dorset-Thule succession in Arctic North America: assessing claims for culture contact. *Am. Antiq.* 58, 203–234.
- Pauly, D., Trites, A.W., Capuli, E., Christensen, V., 1998. Diet composition and trophic levels of marine mammals. *ICES (Int. Counc. Explor. Sea) J. Mar. Sci.* 55, 467–481.
- Pienkowski, A.J., Gill, N.K., Furze, M.F., Mugo, S.M., Marret, F., Perreux, A., 2017. Arctic sea-ice proxies: comparisons between biogeochemical and micro-paleontological reconstructions in a sediment archive from Arctic Canada. *Holocene* 27, 665–682.
- Polyak, L., Alley, R.B., Andrews, J.T., Brigham-Grette, J., Cronin, T.M., Darby, D.A., Dyke, A.S., Fitzpatrick, J.J., Funder, S., Holland, M., Jennings, A.E., Miller, G.H., O'Regan, M., Savelle, J., Serreze, M., St John, K., White, J.W.C., Wolff, E., 2010. History of sea ice in the Arctic. *Quat. Sci. Rev.* 29, 1757–1778.
- Pomeroy, C., Ferguson, S.H., Walkusz, W., 2011. Stomach contents of bowhead whales (*Balaena mysticetus*) from four locations in the Canadian Arctic. *Polar Biol.* 34, 615–620.
- Pomeroy, C., Lesage, V., Ferguson, S.H., Winkler, G., Petersen, S.D., Higdon, J.W., 2012. Prey assemblage isotopic variability as a tool for assessing diet and the spatial distribution of bowhead whale *Balaena mysticetus* foraging in the Canadian eastern Arctic. *Mar. Ecol. Prog. Ser.* 469, 161–174.
- Popp, B.N., Laws, E.A., Bidigare, R.R., Dore, J.E., Hanson, K.L., Wakeham, S.G., 1998. Effect of phytoplankton cell geometry on carbon isotopic fractionation. *Geochim. Cosmochim. Acta* 62, 69–77.
- Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83, 703–718.
- Post, D.M., 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth bass. *Ecology* 84, 1298–1310.
- Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M., Astrup, P., 2009. Ecological dynamics across the arctic associated with recent climate change. *Science* 325, 1355–1358.
- Raghavan, M., DeGorgio, M., Albrechtsen, A., Moltke, I., Skoglund, P., Korneliusen, T.S., Grønnow, B., Appelt, M., Gulløv, H.C., Friesen, T.M., Fitzhugh, W., Malmström, H., Rasmussen, S., Olsen, J., Melchior, L., Fuller, B.T., Fahrni, S.M., Stafford, T., Grimes, V., Renouf, M.A.P., Cybulski, J., Lynnerup, N., Lahr, M.M., Britton, K., Knecht, R., Arneborg, J., Metspalu, M., Cornejo, O.E., Malaspina, A.-S., Wang, Y., Rasmussen, M., Raghavan, V., Hansen, T.V.O., Khushnudinova, E., Pierre, T., Dneprovsky, K., Andreasen, C., Lange, H., Hayes, M.G., Coltrain, J., Spitsyn, V.A., Götherström, A., Orlando, L., Kivisild, T., Villem, R., Crawford, M.H., Nielsen, F.C., Dissing, J., Heinemeier, J., Meldgaard, M., Bustamante, C., O'Rourke, D.H., Jakobsson, M., Gilbert, M.T.P., Nielsen, R., Willerslev, E., 2014. The genetic prehistory of the New World Arctic. *Science* 345, 1020–1029.
- Rau, G.H., Sweeney, R.E., Kaplan, I.R., 1982. Plankton ^{13}C : ^{12}C ratio changes with latitude: differences between northern and southern oceans. *Deep Sea Res. Part A. Oceanographic Research Papers* 29, 1035–1039.
- Raven, J.A., Johnston, A.M., Kübler, J.E., Korb, R., McInroy, S.G., Handley, L.L., Scrimgeour, C.M., Walker, D.J., Beardall, J., Vanderklift, M., Fredriksen, S., Dunton, K.H., 2002. Mechanistic interpretation of carbon isotope discrimination by marine macroalgae and seagrasses. *Funct. Plant Biol.* 29, 355–378.
- Reed, C.A., Braidwood, R.J., 1960. The environmental sequence in northeastern Iraq. In: Braidwood, R.J., Howe, B. (Eds.), *Explorations in Iraqi Kurdistan*. Oriental Institute of the University of Chicago, Chicago, pp. 163–175.
- Reeves, R.R., 1998. Distribution, abundance and biology of ringed seals (*Phoca hispida*): an overview. *NAMMO Sci. Publ.* 1, 9–45.
- Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haffidason, H., Hajdas, I., Hatté, C., Heaton, T.J., Hoffmann, D.L., Hogg, A.G., Hughes, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Staff, R.A., Turney, C.S.M., van der Plicht, J., 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55, 1869–1887.
- Renauld, P.E., Riedel, A., Michel, C., Morata, N., Gosselin, M., Juul-Pedersen, T., Chiuchio, A., 2007. Seasonal variation in benthic community oxygen demand: a response to an ice algal bloom in the Beaufort Sea, Canadian Arctic? *J. Mar. Syst.* 67, 1–12.
- Rick, A.M., 1980. Non-Cetacean vertebrate remains from two Thule winter houses on Somerset Island, N.W.T. *Can. J. Archaeol.* 99–117.
- Riofrío-Lazo, M., Auriolo-Gamboa, D., 2013. Timing of isotopic integration in marine mammal skull: comparative study between calcified tissues. *Rapid Commun. Mass Spectrom.* 27, 1076–1082.
- Ruiz-Cooley, R., Engelhaupt, D., Ortega-Ortiz, J., 2012. Contrasting C and N isotope ratios from sperm whale skin and squid between the Gulf of Mexico and Gulf of

- California: effect of habitat. *Mar. Biol.* 159, 151–164.
- Ruiz-Cooley, R.L., Gerrodette, T., 2012. Tracking large-scale latitudinal patterns of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ along the E Pacific using epi-mesopelagic squid as indicators. *Ecosphere* 3, 1–17.
- Savelle, J.M., 1997. The role of architectural utility in the formation of zooarchaeological whale bone assemblages. *J. Archaeol. Sci.* 24, 869–885.
- Savelle, J.M., 2002. Logistical organization, social complexity, and the collapse of prehistoric Thule whaling societies in the Central Canadian Arctic Archipelago. In: Fitzhugh, B., Habu, J. (Eds.), *Beyond Foraging and Collecting: Evolutionary Change in Hunter-Gatherer Settlement Systems*. Kluwer Academic, New York, pp. 73–90.
- Savelle, J.M., 2010. Cumulative bowhead whale (*Balaena mysticetus*) harvest estimates by prehistoric Thule Inuit in the Canadian Arctic 1200–1500 A.D.: implications for bowhead whale population modeling and Thule demography. *Bulletin Natl. Mus. Ethnol.* 34, 593–618.
- Savelle, J.M., Dyke, A.S., 2002. Variability in Palaeoeskimo occupation on southwestern Victoria Island, Arctic Canada: causes and consequences. *World Archaeol.* 33, 508–522.
- Savelle, J.M., Dyke, A.S., 2009. Palaeoeskimo demography on Western Boothia Peninsula, Arctic Canada. *J. Field Archaeol.* 34, 267–283.
- Savelle, J.M., Dyke, A.S., 2014. Palaeoeskimo occupation history of Foxe Basin, Arctic Canada: implications for the core area model and Dorset origins. *Am. Antiq.* 79, 249–276.
- Savelle, J.M., Dyke, A.S., Whitridge, P.J., Poupart, M., 2012. Palaeoeskimo demography on western Victoria island, Arctic Canada: implications for social organization and longhouse development. *Arctic* 65, 167–181.
- Savelle, J.M., Habu, J., 2004. A processual investigation of a Thule whale bone house, Somerset Island, Arctic Canada. *Arctic Anthropol.* 41, 204–221.
- Savelle, J.M., McCartney, A.P., 1988. Geographic and temporal variation in Thule eskimo subsistence economies: a model. *Res. Econ. Anthropol.* 10, 21–72.
- Schaal, G., Nerot, C., Grall, J., Chouvelon, T., Lorrain, A., Mortillaro, J.-M., Savoye, N., Brind'Amour, A., Paulet, Y.-M., Le Bris, H., 2016. Stable isotope ratios in benthomeres biota along a depth gradient in the Bay of Biscay: a multitrophic study. *Estuar. Coast Shelf Sci.* 179, 201–206.
- Schell, D.M., 2000. Declining carrying capacity in the Bering Sea: isotopic evidence from whale baleen. *Limnol. Oceanogr.* 45, 459–462.
- Schell, D.M., 2001. Carbon isotope ratio variations in Bering Sea biota: the role of anthropogenic carbon dioxide. *Limnol. Oceanogr.* 46, 999–1000.
- Schledermann, P., 1979. The "Baleen" Period of the Arctic whale hunting tradition. In: McCartney, A.P. (Ed.), *Thule Eskimo Culture: an Anthropological Retrospective*. National Museums of Canada, Ottawa, pp. 134–148.
- Schledermann, P., 1980. Polynyas and prehistoric settlement patterns. *Arctic* 33, 292–302.
- Schwarcz, H.P., 1991. Some theoretical aspects of isotope paleodiet studies. *J. Archaeol. Sci.* 18, 261–275.
- Screen, J.A., Deser, C., Smith, D.M., Zhang, X., Blackport, R., Kushner, P.J., Oudar, T., McCusker, K.E., Sun, L., 2018. Consistency and discrepancy in the atmospheric response to Arctic sea-ice loss across climate models. *Nat. Geosci.* 11, 155–163.
- Screen, J.A., Simmonds, I., 2010. The central role of diminishing sea ice in recent Arctic temperature amplification. *Nature* 464, 1334–1337.
- Seddon, A.W.R., Macias-Fauria, M., Long, P.R., Benz, D., Willis, K.J., 2016. Sensitivity of global terrestrial ecosystems to climate variability. *Nature* 531, 229.
- Serreze, M.C., Barrett, A.P., Stroeve, J.C., Kindig, D.N., Holland, M.M., 2009. The emergence of surface-based Arctic amplification. *Cryosphere* 3, 11–19.
- Serreze, M.C., Barry, R.G., 2011. Processes and impacts of Arctic amplification: a research synthesis. *Glob. Planet. Chang.* 77, 85–96.
- Sherwood, O.A., Guilderson, T.P., Batista, F.C., Schiff, J.T., McCarthy, M.D., 2014. Increasing subtropical north Pacific Ocean nitrogen fixation since the Little Ice Age. *Nature* 505, 78–81.
- Sherwood, O.A., Lehmann, M.F., Schubert, C.J., Scott, D.B., McCarthy, M.D., 2011. Nutrient regime shift in the western North Atlantic indicated by compound-specific $\delta^{15}\text{N}$ of deep-sea gorgonian corals. *Proc. Natl. Acad. Sci.* 108, 1011–1015.
- Siegstad, H., Neve, P.B., Heide-Jørgensen, M.P., Härkönen, T., 1998. Diet of the ringed seal (*Phoca hispida*) in Greenland. *NAMMO Sci. Publ.* 1, 229–241.
- Sigman, D.M., Karsh, K.L., Casciotti, K.L., 2009. Nitrogen isotopes in the ocean. In: Steele, J.H., Turekian, K.K., Thorpe, S.A. (Eds.), *Encyclopedia of Ocean Sciences*, second ed. Academic Press, San Diego, pp. 40–54.
- Smith, T.G., Hammill, M.O., Taubøl, G., 1991. A review of the developmental, behavioural and physiological adaptations of the ringed seal, *Phoca hispida*, to life in the arctic winter. *Arctic* 44, 124–131.
- Smith, T.G., Stirling, I., 1975. The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. *Can. J. Zool.* 53, 1297–1305.
- Sørdeide, J.E., Carroll, M.L., Hop, H., Ambrose, W.G., Hegseth, E.N., Falk-Petersen, S., 2013. Sympagic-pelagic-benthic coupling in Arctic and Atlantic waters around Svalbard revealed by stable isotopic and fatty acid tracers. *Mar. Biol. Res.* 9, 831–850.
- Sørdeide, J.E., Falk-Petersen, S., Hegseth, E.N., Hop, H., Carroll, M.L., Hobson, K.A., Blachowiak-Samolyk, K., 2008. Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 55, 2225–2244.
- Sørdeide, J.E., Hop, H., Carroll, M.L., Falk-Petersen, S., Hegseth, E.N., 2006. Seasonal food web structures and sympagic–pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. *Prog. Oceanogr.* 71, 59–87.
- Sørdeide, J.E., Leu, E.V.A., Berge, J., Graeve, M., Falk-Petersen, S., 2010. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Glob. Chang. Biol.* 16, 3154–3163.
- Stirling, I., 1980. The biological importance of polynyas in the Canadian Arctic. *Arctic* 33, 303–315.
- Stirling, I., 1997. The importance of polynyas, ice edges, and leads to marine mammals and birds. *J. Mar. Syst.* 10, 9–21.
- Stroeve, J., Holland, M.M., Meier, W., Scambos, T., Serreze, M., 2007. Arctic sea ice decline: faster than forecast. *Geophys. Res. Lett.* 34, L09501.
- Stroeve, J.C., Serreze, M.C., Holland, M.M., Kay, J.E., Malanik, J., Barrett, A.P., 2012. The Arctic's rapidly shrinking sea ice cover: a research synthesis. *Clim. Change* 110, 1005–1027.
- Sundqvist, H.S., Kaufman, D.S., McKay, N.P., Balascio, N.L., Briner, J.P., Cwynar, L.C., Sejrup, H.P., Seppä, H., Subetto, D.A., Andrews, J.T., Axford, Y., Bakke, J., Birks, H.J.B., Brooks, S.J., de Vernal, A., Jennings, A.E., Ljungqvist, F.C., Rühland, K.M., Saenger, C., Smol, J.P., Viau, A.E., 2014. Arctic Holocene proxy climate database – new approaches to assessing geochronological accuracy and encoding climate variables. *Clim. Past* 10, 1605–1631.
- Szpak, P., Buckley, M., Darwent, C.M., Richards, M.P., 2018. Long-term ecological changes in marine mammals driven by recent warming in northwestern Alaska. *Glob. Chang. Biol.* 24, 490–503.
- Szpak, P., Krippner, K., Richards, M.P., 2017a. Effects of sodium hydroxide treatment and ultrafiltration on the removal of humic contaminants from archaeological bone. *Int. J. Osteoarchaeol.* 27, 1070–1077.
- Szpak, P., Metcalfe, J.Z., Macdonald, R.A., 2017b. Best practices for calibrating and reporting stable isotope measurements in archaeology. *J. Archaeol. Sci.: Reports* 13, 609–616.
- Szpak, P., Orchard, T.J., McKechnie, I., Gröcke, D.R., 2012. Historical ecology of late Holocene sea otters (*Enhydra lutris*) from northern British Columbia: isotopic and zooarchaeological perspectives. *J. Archaeol. Sci.* 39, 1553–1571.
- Szpak, P., Orchard, T.J., Salomon, A.K., Gröcke, D.R., 2013. Regional ecological variability and impact of the Maritime Fur Trade on nearshore ecosystems in southern Haida Gwaii (British Columbia, Canada): evidence from stable isotope analysis of rockfish (*Sebastes* spp.) bone collagen. *Archaeol. Anthropol. Sci.* 5, 159–182.
- Takai, N., Onaka, S., Ikeda, Y., Yatsu, A., Kidokoro, H., Sakamoto, W., 2000. Geographical variations in carbon and nitrogen stable isotope ratios in squid. *J. Mar. Biol. Assoc. U. K.* 80, 675–684.
- Tameler, T., Renaud, P.E., Hop, H., Carroll, M.L., William, G., Ambrose, J., Hobson, K.A., 2006. Trophic relationships and pelagic-benthic coupling during summer in the Barents Sea Marginal Ice Zone, revealed by stable carbon and nitrogen isotope measurements. *Mar. Ecol. Prog. Ser.* 310, 33–46.
- Thomas, E.K., Szymanski, J., Briner, J.P., 2010. Holocene alpine glaciation inferred from lacustrine sediments on northeastern Baffin Island, Arctic Canada. *J. Quat. Sci.* 25, 146–161.
- Timpson, A., Colledge, S., Crema, E., Edinborough, K., Kerig, T., Manning, K., Thomas, M.G., Shennan, S., 2014. Reconstructing regional population fluctuations in the European Neolithic using radiocarbon dates: a new case-study using an improved method. *J. Archaeol. Sci.* 52, 549–557.
- Tivy, A., Howell, S.E.L., Alt, B., McCourt, S., Chagnon, R., Crocker, G., Carrieres, T., Yackel, J.J., 2011. Trends and variability in summer sea ice cover in the Canadian Arctic based on the Canadian Ice Service Digital Archive, 1960–2008 and 1968–2008. *J. Geophys. Res.: Oceans* 116, C03007.
- Tremblay, G., Belzile, C., Gosselin, M., Poulin, M., Roy, S., Tremblay, J.E., 2009. Late summer phytoplankton distribution along a 3500 km transect in Canadian Arctic waters: strong numerical dominance by picoeukaryotes. *Aquat. Microb. Ecol.* 54, 55–70.
- Tynan, C.T., Ainley, D.G., Stirling, I., 2010. Sea ice: a critical habitat for polar marine mammals and birds. In: Thomas, D.N., Dieckmann, G.S. (Eds.), *Sea Ice*, second ed. Wiley, West Sussex, UK, pp. 395–424.
- Ukkonen, P., Aaris-Sørensen, K., Arppe, L., Daugnor, L., Halkka, A., Löugas, L., Oinonen, M.J., Pilot, M., Storå, J., 2014. An Arctic seal in temperate waters: history of the ringed seal (*Pusa hispida*) in the Baltic Sea and its adaptation to the changing environment. *Holocene* 24, 1694–1706.
- Vales, D.G., Cardona, L., Zangrando, A.F., Borella, F., Saporiti, F., Goodall, R.N.P., de Oliveira, L.R., Crespo, E.A., 2017. Holocene changes in the trophic ecology of an apex marine predator in the South Atlantic Ocean. *Oecologia* 183, 555–570.
- van Klinken, G.J., 1999. Bone collagen quality indicators for palaeodietary and radiocarbon measurements. *J. Archaeol. Sci.* 26, 687–695.
- Vander Zanden, M.J., Clayton, M.K., Moody, E.K., Solomon, C.T., Weidel, B.C., 2015. Stable isotope turnover and half-life in animal tissues: a literature synthesis. *PLoS One* 10, e0116182.
- Vander Zanden, M.J., Rasmussen, J.B., 2001. Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: implications for aquatic food web studies. *Limnol. Oceanogr.* 46, 2061–2066.
- Vare, L.L., Massé, G., Gregory, T.R., Smart, C.W., Belt, S.T., 2009. sea ice variations in the central Canadian Arctic Archipelago during the Holocene. *Quat. Sci. Rev.* 28, 1354–1366.
- Vinther, B.M., Andersen, K.K., Jones, P.D., Briffa, K.R., Cappelen, J., 2006. Extending Greenland Temperature Records into the Late Eighteenth Century, p. 111.
- Voss, M., Dippner, J.W., Montoya, J.P., 2001. Nitrogen isotope patterns in the oxygen-deficient waters of the eastern tropical North Pacific Ocean. *Deep Sea Res. Oceanogr. Res. Pap.* 48, 1905–1921.
- Wallace, B.P., Seminoff, J.A., Kilham, S.S., Spotila, J.R., Dutton, P.H., 2006. Leatherback turtles as oceanographic indicators: stable isotope analyses reveal a trophic dichotomy between ocean basins. *Mar. Biol.* 149, 953–960.

- Wang, S.W., Springer, A.M., Budge, S.M., Horstmann-Dehn, L., Quakenbush, L.T., Wooller, M.J., 2016. Carbon sources and trophic relationships of ice seals during recent environmental shifts in the Bering Sea. *Ecol. Appl.* 26, 830–845.
- Welch, H.E., Bergmann, M.A., Siferd, T.D., Martin, K.A., Curtis, M.F., Crawford, R.E., Conover, R.J., Haakon, H., 1992. Energy flow through the marine ecosystem of the Lancaster Sound region, Arctic Canada. *Arctic* 45, 343–357.
- Welch, H.E., Crawford, R.E., Haakon, H., 1993. Occurrence of arctic cod (*Boreogadus saida*) schools and their vulnerability to predation in the Canadian High Arctic. *Arctic* 46, 331–339.
- Werner, I., 1997. Grazing of Arctic under-ice amphipods on sea-ice algae. *Mar. Ecol. Prog. Ser.* 160, 93–99.
- Wiencke, C., Fischer, G., 1990. Growth and stable carbon isotope composition of cold-water macroalgae in relation to light and temperature. *Mar. Ecol. Prog. Ser.* 65, 283–292.
- Wiley, A.E., Ostrom, P.H., Welch, A.J., Fleischer, R.C., Gandhi, H., Southon, J.R., Stafford, T.W., Penniman, J.F., Hu, D., Duvall, F.P., James, H.F., 2013. Millennial-scale isotope records from a wide-ranging predator show evidence of recent human impact to oceanic food webs. *Proc. Natl. Acad. Sci. Unit. States Am.* 110, 8972–8977.
- Young, B.G., Ferguson, S.H., 2013. Seasons of the ringed seal: pelagic open-water hyperphagy, benthic feeding over winter and spring fasting during molt. *Wildl. Res.* 40, 52–60.
- Yurkowski, D.J., Ferguson, S.H., Semeniuk, C.A.D., Brown, T.M., Muir, D.C.G., Fisk, A.T., 2016. Spatial and temporal variation of an ice-adapted predator's feeding ecology in a changing Arctic marine ecosystem. *Oecologia* 180, 631–644.